

ECOLOGY OF *RUPPIA MARITIMA* L. IN NEW HAMPSHIRE (U.S.A) TIDAL MARSHES¹

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Ruppia maritima L. is a submersed aquatic angiosperm of saline environments. The taxonomy of this nearly cosmopolitan genus has been the subject of numerous studies although no definitive classification of the various taxa has been established. *Ruppia* has been placed in the monogeneric family, Ruppiales, by Hutchinson (1934, 1959). It has also been included in the Potamogetonaceae, Zosteraceae, and Najadaceae. Davis and Tomlinson (1974) reviewed the systematic position of *Ruppia*. Similarities between *Ruppia* and *Potamogeton* in vegetative morphology, anatomy, and especially floral morphology (Uhl, 1947; Posluszny & Sattler, 1974) appear to outweigh dissimilarities, hereby substantiating its inclusion in the Potamogetonaceae. A number of varieties of *R. maritima* based on morphological criteria have been described for Eastern North America by Fernald and Wiegand (1914).

Ruppia grows in a wide diversity of coastal and estuarine habitats in New Hampshire. It is commonly found in the relatively still water of shallow pannes or in deeper pools, but may also occur in drainage ditches and occasionally in creeks which ebb and flow with each tide. *Ruppia* is highly variable in growth form, apparently due to changes in environmental conditions at different locations. Factors such as depth of water, temperature, salinity, and structural characteristics of the habitat, together with biotic and physicochemical parameters, significantly influence its growth, development, and reproductive biology. Under certain conditions *Ruppia* may exist as a perennial by means of vegetative reproduction and overwintering rhizomes, or it may employ an annual reproductive strategy producing abundant seed.

A number of investigators have reported on environmental conditions and growth of *Ruppia*, but the relationship between environmental parameters and clinal variation in *Ruppia* populations has not been established. Setchell (1924, 1946) studied *Ruppia maritima*

¹Scientific contribution Number 997 from the New Hampshire Agricultural Experiment Station. Accepted for publication August 8, 1979.

L. and *R. spiralis* Dumort. and their environmental factors in California. Many of my findings on seasonal periodicity and temperature and salinity optima concur with his. Setchell's treatment, unfortunately, embodies no graphical presentation of his data with which quantitative comparisons can be made. Joanen (1964) studied factors influencing the establishment of natural and artificial stands of *Ruppia maritima* L. in Louisiana. Gore (1965) studied the effects of small salt marsh impoundments on *Ruppia* sp. in Maine. Bourn (1935) conducted greenhouse experiments on *Ruppia maritima* L. which originated on Martha's Vineyard, Massachusetts, to determine sea-water tolerance. McKay (1935) investigated lakes of high magnesium sulfate content in Washington and British Columbia to assess the salt tolerance of *Ruppia maritima* L. Mayer (1967, 1969) studied the effect of salinity on growth, reproduction, and fruit size in *Ruppia maritima* L. Verhoeven (1975) and Verhoeven and van Vierssen (1978) have examined the distribution and structure of communities consisting of three taxa of *Ruppia* [*R. cirrhosa* (Petag.) Grande, *R. maritima* L., and *R. maritima* var. *brachypus* (Gay) Marsson] in relation to salinity and salinity fluctuations in the Camargue, France, and at "De Bol", Texel, The Netherlands. Verhoeven (1978) found that natural regulation of plant biomass in *Ruppia*-dominated communities is a seasonal phenomenon involving biotic and abiotic factors. Davis and Tomlinson (1974) reported a new species of *Ruppia* (*R. tuberosa* Davis & Tomlinson) growing in very high salinity (92–132 ‰) in Western Australia. Gutierrez (1977) investigated the asynchronous development of *Ruppia maritima* L. beds in a coastal lagoon in Mexico and found that changes in turbidity, currents, soil pH and texture, as well as fluctuations in temperature and salinity, differentially affect growth and vegetative propagation. Graves (1908) presented information on salinity tolerances and halophytic adaptations in a detailed study of the morphology of *Ruppia maritima* L.

This paper reports on selected environmental parameters and salient features of the habitats of *Ruppia* in an effort to contribute to an understanding of the dynamics of these habitats as integral parts of the tidal marsh ecosystem. These data, when correlated with information on the growth and development of the *Ruppia* populations indigenous to various habitats, provide insight to the morphological variability and the reproductive strategies observed in this species as a function of its environment.

MATERIALS AND METHODS

Selection of Sites

A reconnaissance of various *Ruppia* habitats was conducted during the summer and fall of 1973 while making a soil survey of New Hampshire tidal marshes (Breeding et al., 1974). Approximately thirty sites were observed for: (1) type of habitat; (2) water depth, temperature, and salinity; (3) composition of the substrate; (4) characteristics of the *Ruppia* population; (5) surrounding vegetation. Ultimately, ten sites were selected as representing a range of ecologically distinct habitats of *Ruppia maritima* (Fig. 1). Plants at these sites exhibited variation in growth habit conforming to three varieties (vars. *rostrata* Agardh, *longipes* Hagstr., and *subcapitata* Fern. & Wieg.) described by Fernald and Wiegand (1914). The sites were monitored during the growing season of *Ruppia* (mid-April to early September) in 1974 and 1975. Seven of the ten sites in 1974 and five in 1975 were visited every week to ten days, the others less frequently. A comparison of five representative sites is presented in this paper. For more detailed information see Richardson (1976a). All sites were visited between 10:00 a.m. and 3:00 p.m. on the same day, each within a specified time. At each site all measurements were made at a place designated by a marker. Collections of *Ruppia* were made at each of the regularly sampled sites throughout the study period.

Seasonal Studies (April–September 1974 and 1975)

Water Depth: Fluctuations in water depth as an expression of the effects of flooding tides, precipitation, and evaporation were measured with a meter stick alongside the permanent marker at each site.

Temperature: Air and water temperatures were measured with an adjustable boom apparatus which could be lowered to the required depth. Copper vs. constantan thermocouple wires were attached to a vertical probe by rubber bands so that they could be adjusted to divide the depth of the water column into equal increments no more than 10 cm apart. The thermocouple wires were joined to a multiple switch which was connected to a Leeds and Northrup millivolt potentiometer via an Omega-CJ cold junction compensator. Temperature stratification in the water column could be measured accurately with this apparatus.

Salinity: A Yellow Springs Inst. model 33 S-C-T meter was used to measure salinity at the same series of depths at which temperature readings were taken. The instrument was periodically standardized against a silver nitrate titration of sea water (Strickland & Parsons, 1968).

Oxygen content: Dissolved oxygen (D.O.) values were determined by the Winkler method (A.P.H.A., 1971; Strickland & Parsons, 1968) using Hach dry chemical pillows for the three fixation reagents. Water was collected just below the surface, therefore the D.O. values expressed in this paper do not represent an average for the entire water column but, nevertheless, do give an approximation of the seasonal patterns at different sites.

Precipitation data were obtained from the Durham, New Hampshire weather station. Information on tidal periodicity and photoperiod was taken from U.S.D.C., N.O.A.A. tide tables (Anon., 1974, 1975). Estimates of percent cover by algal mats, epibiota, turbidity, and conditions of the substrate (e.g., color as an indication of the degree of reducing conditions) were made on a comparative basis on each visit to a site.

Ten Day Study (Vols Island, July 22–31, 1974)

To determine what sort of changes occurred between sampling days and to obtain data on diel fluctuations of the physicochemical parameters a ten day study was conducted. Vols Island was selected as a representative site which was easily accessible for thrice daily visits. The study began shortly after flood tides had filled the pool to near maximum so that the effects of evaporation during the following neap tide period could be observed. For nine days the site was visited at 6:00 am, 12:00 am and 6:00 pm; on the tenth day hourly measurements were taken over a twelve hour period to record diurnal fluctuations.

In addition to the parameters recorded in the seasonal studies, during the ten day study, pH values were measured with a VWR Scientific solid state pH meter standardized before each reading with a buffer solution. Two replicates of three readings (open water, moderate plant cover, and dense plant cover) were taken to record a pH range. All readings were taken at 5 cm below the water surface. Incident radiation was recorded with an Argomet—Lintronic dome solarimeter connected to the millivolt potentiometer. Radiation values represent an average of readings over a ten minute period.

DESCRIPTION OF STUDY AREAS

1. Johnson Creek

Location: Durham, New Hampshire (43° 9'N, 70° 54'W)

Habitat type: A vertically sided pool with undercut banks, measuring 24 m × 7 m, situated on the inner bend of a creek meander in proximity to upland drainage.

Substrate: The bottom of this pool is extremely soft, deep organic muck. Black color indicated reducing conditions. The plants were deeply rooted but could be easily pulled up without damage to the roots.

Characteristics of the *Ruppia* population: A dense growth of plants conforming to var. *rostrata* was found at this site (Fig. 9,A). Most flowers appeared to be pollinated underwater. The plants fruited abundantly during the 1974 and 1975 seasons and produced large quantities of seed. An annual reproductive strategy appeared most successful at this site. Lower portions of the plants supported a growth of epiphytes (diatoms, blue-green algae, and other epibiota) by mid-summer. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The pool is bordered with a 1–2 m wide band of *Scirpus paludosus* Nels. on a *Spartina patens* (Ait.) Muhl. high marsh. Dense mats of filamentous algae (*Cladophora* sp. most abundant) covered nearly 90% of the water surface by late summer of 1974 and 1975.

2. Lubberland Creek

Location: Newmarket, New Hampshire (43° 5'N, 70° 55'W)

Habitat type: Extensive shallow pannes have formed in the areas between drainage ditches which have become impounded by slumping of the banks or by siltation. This site receives some upland drainage in the spring, but probably little or none in the summer.

Substrate: Standing surface water has caused differential decay of the underlying peat so that some areas have a relatively firm bottom while others are soft and highly decomposed. The plants became firmly rooted in the peat sod early in the season and could not easily be removed without damage to the roots.

Characteristics of the *Ruppia* population: A dense growth of plants at this site appeared to be intermediate between var. *rostrata* and var. *subcapitata* (Fig. 9,B). The entire population appeared to

be pollinated underwater and formed abundant fruit. The reproductive strategy was primarily annual. The plants flowered and fruited early in the season, produced abundant seed and died off completely by late summer. Relatively few epiphytes were noticed until the plants were senescent. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: Large areas of these pannes are covered with *Scirpus paludosus* growing in standing water. Narrow bands of *Spartina patens* persist along the edges of the ditches on levees where fine sediments are trapped during flood tides. 50–80% of the surface area of the pannes was covered with filamentous algal mats by mid-summer.

3. Vols Island

Location: Newmarket, New Hampshire (43° 5'N, 70° 54'W)

Habitat type: A pool with nearly vertical sides, measuring 10 m × 2 m, was determined to be a relict of a former creek meander from interpretation of aerial photographs and sounding the marsh soil. Situated on the high marsh, the site receives some upland drainage in the spring.

Substrate: The plants were loosely rooted in very soft deep organic ooze containing fractions of silt and clay. Black color was indicative of reducing conditions in the mud.

Characteristics of the *Ruppia* population: A fairly dense growth of plants conforming to var. *rostrata*, but with highly variable fruit shape, was present at this site (Fig. 9,C). Underwater pollination was dominant. An annual reproductive strategy was evident here as the pool contained only seed in early spring. The plants were nearly free of epiphytes throughout the season. Phenological data are given in Table 3 and 4.

Surrounding vegetation: A vigorous stand of *Spartina patens* surrounds the pool. A very dense mat of filamentous algae covered nearly 100% of the surface area by mid to late summer during both seasons.

4. Awcomin Marsh (deep pool)

Location: Rye, New Hampshire (43° 1'N, 70° 44'W)

Habitat type: A large, deep pool measuring 30 m × 6 m, with vertical sides, may have been formed, with others in the vicinity, as a primary panne on the intertidal marsh (see Redfield, 1972). Situated on a large flat expanse of tidal marsh, the pool receives virtually no upland runoff and is isolated from large creeks.

Substrate: One end of the pool has a firm sandy bottom with few plants. The remaining portion consists of a deposit of soft mud and organic matter overlying sand which provided a rooting medium for the large population of plants growing there in 1974. The mud was grey-brown, apparently not highly reduced.

Characteristics of the *Ruppia* population: In 1974 a dense growth of *Ruppia* with long flexuous to straight peduncles conforming to var. *longipes* was observed (Fig. 9,D). The plants in early spring of 1974 were well developed and covered with epiphytes, indicating that they had persisted from the previous season. Renewal growth was observed in the axils of leaves and from rhizomes producing new shoots and inflorescences. Pollination occurred almost exclusively at the water surface. Few fruits were formed, however, and the plants became senescent in late summer. In early spring of 1975 the pool was nearly devoid of living *Ruppia*. There was no reestablishment of growth from either seed or vegetative propagation during the 1975 season. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The dwarf form of *Spartina alterniflora* borders the pool. In 1974 filamentous algal mats covered about 30% of the surface. In 1975 there was almost no growth of filamentous algae.

5. **Awcomin Marsh** (shallow panne)

Location: Rye, New Hampshire (43° 1'N, 70° 44'W) about 100 m west of the deep pool.

Habitat type: Unlike the deep pool, this large, shallow panne appears to be a secondary formation on the marsh surface (see Redfield, 1972) as the standing water is gradually decomposing the underlying peat.

Substrate: Approximately 10–15 cm of decomposing peat and sticky organic mud overlies coarse intertidal peat. Beneath a thin surface layer of detritus the mud was black, indicating reducing conditions.

Characteristics of the *Ruppia* population: In 1974 the vegetative portions of the plants were very similar to those in the deep pool; however, the peduncle lengths were highly variable and many more fruits were produced (Fig. 9,E). Pollination appeared to be entirely at the surface and, on occasion, masses of floating pollen were seen. The lower portions of the plants were covered with epiphytes in early spring, again giving evidence of persistence of a previous season's growth. As in the deep pool, this panne was entirely devoid of

Ruppia plants in 1975. Although fruits were produced in 1974, no seedlings were found in 1975. Phenological data are given in Tables 3 and 4.

Surrounding vegetation: The dwarf form of *Spartina alterniflora* borders the panne. Very scant growth of filamentous algae was noted during both seasons.

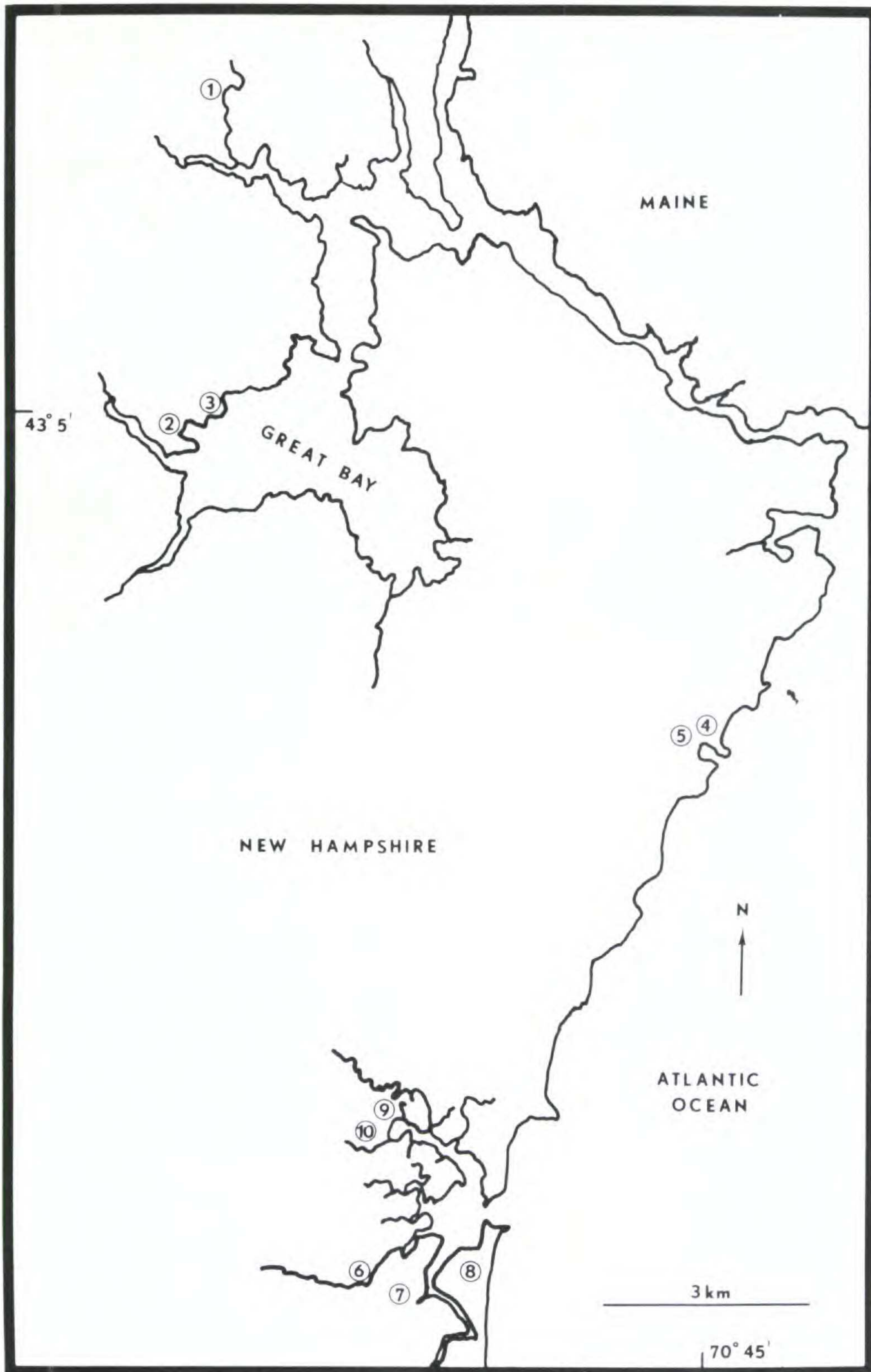
RESULTS AND DISCUSSION

Seasonal Studies

Water Depth: Verhoeven (1975) stressed the importance of evaporation to the aquatic environment since it results in lowering the water level, increasing the salinity, and subsequently increasing the chance of desiccation. Large shallow pannes such as those at Lubberland Creek had more rapid fluctuations in depth than deeper pools due to higher rates of evaporation from a large surface area with relatively small volume. Portions of the pannes at Lubberland Creek were frequently exposed with the mud surface drying, although a small amount of water usually remained under the mats of filamentous algae. This water protects the underlying *Ruppia* from desiccation. Rainfall and tidal flooding allowed for continued growth and development of the plants early in the season when the drying period was not prolonged. Maturation of fruits was observed to be rapid after reflooding.

Drying conditions in late summer, however, caused complete desiccation in the shallow pannes, but only after seeds had formed and become buried in the sediments or entangled in the algal mats. Seeds were very seldom found to be completely dried as there was moisture under the encrusted surface layer of mud and algae. *Ruppia* seeds, like those of most submersed aquatics, lose viability with prolonged drying (see Crocker, 1907; Guppy, 1897; Joanen, 1964; McLaughlin, 1974; Muenscher, 1936). McLaughlin reports that differential drying or non-drying requirements for three species of *Callitriche* are dependent on temperature, salinity, and seasonal phenomena at various habitats. Guppy indicates that drying requirements are characteristic of aquatic species in habitats subject to

Figure 1. Location map of study areas on New Hampshire tidal marshes: 1, Johnson Creek site, 2, Lubberland Creek site, 3, Vols Island site, 4, Awcomin Marsh sites, 5, Taylor River sites, 6, Cains Creek site, 7, Waltons Landing site, 8, Seabrook Dunes site, 9 & 10 Taylor River sites.



periodic drying, but not characteristic of species indigenous to continuously wet habitats. An annual reproductive strategy is imperative to insure survival of *Ruppia* populations in areas where drying conditions are prevalent in late summer. The fragile, herbaceous portions of the plants, subject to complete desiccation, will persist only in a perpetually wet environment. Perennating rhizomes were found only in deeper pools and continuously wet habitats.

In deeper, vertically sided pools which do not receive frequent tidal inundation, some water loss may occur by transference into the surrounding peat soil as the interstitial water level drops during neap tide periods (see Chapman, 1938, 1940, 1960; Redfield, 1959, 1965). Surface algal mats tend to keep the underlying water cool and diminish the effect of wind on evaporation. On hot dry days, dense algal mats may have a wick effect, causing considerable water loss. The effects of evaporation were more apparent in 1974 than in 1975, due largely to differences in precipitation. Rainfall was 21.9 cm during the 1974 study period and 45.6 cm during the 1975 period.

The growth habit of *Ruppia* on New Hampshire tidal marshes is markedly influenced by water depth. Plants growing in shallow pannes exhibit a procumbent spreading habit with distinctly forking stems (Fig. 9,C) while those growing in deeper water are more ascending (Fig. 9,A). Internodal lengths are shorter on shallow water plants than on those growing in deeper areas. Inflorescences usually develop at the second or third node above the rhizome on shallow water plants while those of deeper water plants appear at the fifth or sixth nodes. As plants in deeper pools grow up through the water towards the surface the internodes become progressively shorter. In plants pollinated underwater, peduncle length varies little regardless of depth except for plants in very shallow pannes (which conform to var. *subcapitata*). Plants in which pollination occurs at the surface exhibit highly variable peduncle length. This variability is, presumably, a function of the distance between the point of origin of the inflorescence and the surface of the water.

Temperature: Seasonal temperature patterns at the various sites were similar, and the seasonal mean water temperature for all sites fell within a range of 5° C in 1974 and 1975. However, the thermal regime for each site varied according to its structural characteristics and the distribution of vegetation (Figs. 2 and 3). Temperature stratification occurred at some sites while others remained nearly

isothermal. Sites exhibiting temperature stratification frequently showed salinity stratification as well, whereas those with isothermal conditions were usually isohaline.

Thermal optima for germination, vegetative growth, flowering and fruiting of *Ruppia* were similar at all sites. Seed germination occurred over a range of 11–18°C. Seedling development and vegetative growth appeared to be most vigorous at 20–25°C. Flowering and pollination occurred at 24–30°C. Fruit development, maturation and seed production were observed to occur over a range of 26–32°C. These data compare with those of other workers.

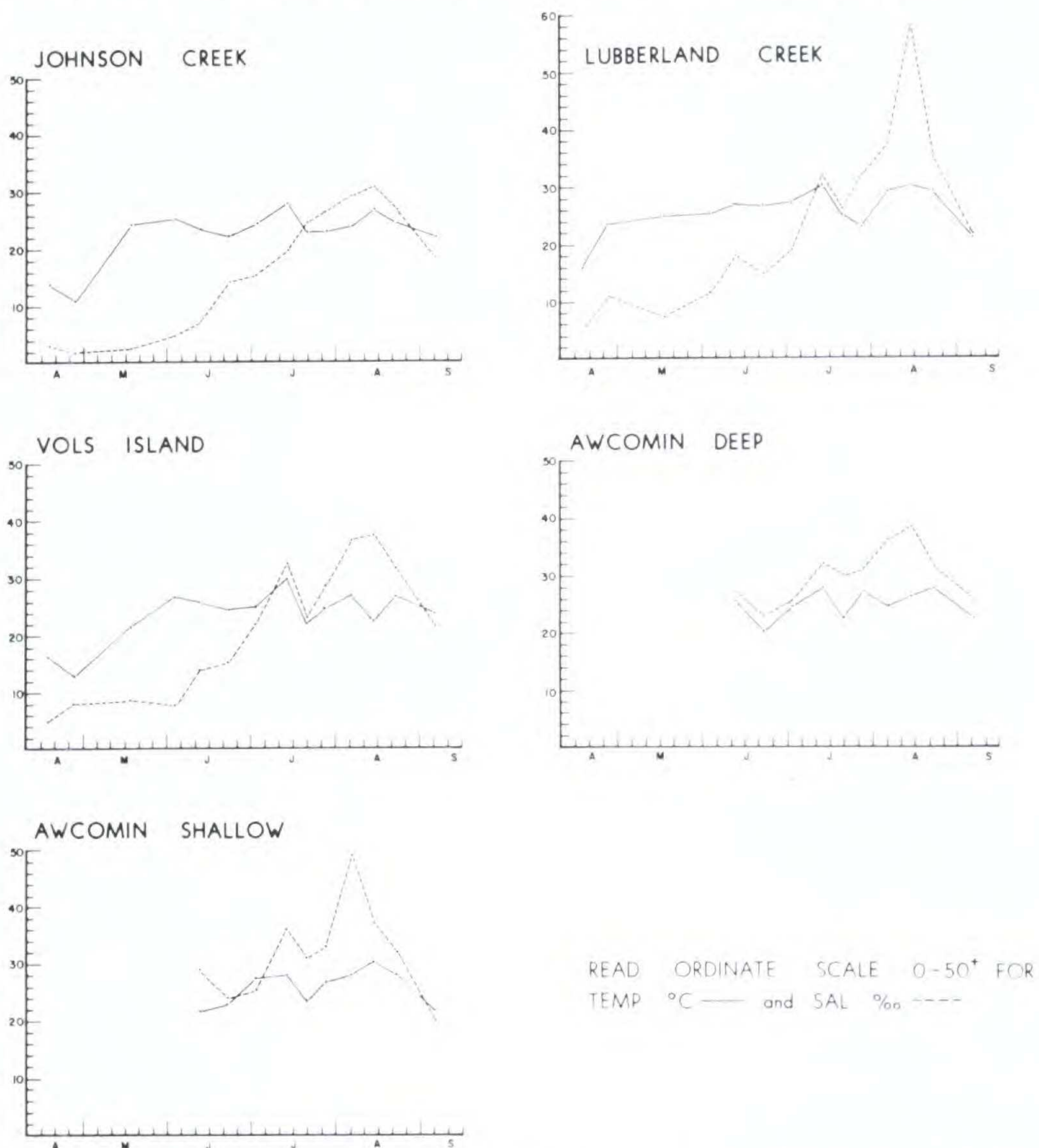


Figure 2. Seasonal water temperature and salinity patterns at five sites April-September 1974.

Table 1. Seasonal ranges and means of water depth, temperature, and salinity for five sites April-September 1974 and 1975

	1974				1975							
	Depth(cm)		Temp.(°C)		Sal.(0/00)		Depth(cm)		Temp.(°C)		Sal.(0/00)	
	R	\bar{X}	R	\bar{X}	R	\bar{X}	R	\bar{X}	R	\bar{X}	R	\bar{X}
JOHNSON CREEK	20-32	27.5	11-28	22.0	2-31	15.0	26-34	30.5	13-34	24.5	2-26	15.9
LUBBERLAND CREEK	5-18	11.8	16-30	27.2	5-58	22.2	14-22	17.4	11-37	26.7	13-37	23.0
VOLS ISLAND	10-30	23.1	11-30	23.2	3-39	21.9	18-32	26.2	12-32	24.5	7-33	20.0
AWCOMIN (DEEP)	28-56*	46.5	19-29*	24.9	23-38*	32.9	38-60	52.8	12-34	24.1	22-35	30.0
AWCOMIN (SHALLOW)	9-28*	20.4	22-30*	26.0	20-49*	31.7	11-26	20.8	15-38	26.6	23-35	29.5

*Measurements at the Awcomin site commenced four weeks later than the other sites in 1974.

Joanen (1964) reported 18–19° C as the thermal optimum for seedling development with temperatures up to 30° C being conducive to vegetative growth. He observed that flowering and fruiting began at 28–30° C and continued under a higher temperature than did vegetative growth.

Setchell (1924) reported that the progression from germination to anthesis and fruiting proceeds with a general rise in temperature, and that cessation of activity coincides with the advent of cold weather. He reported that seeds germinated at 10–18° C, but that development beyond the vegetative stage did not take place until the temperature reached 22–24° C and then development proceeded to

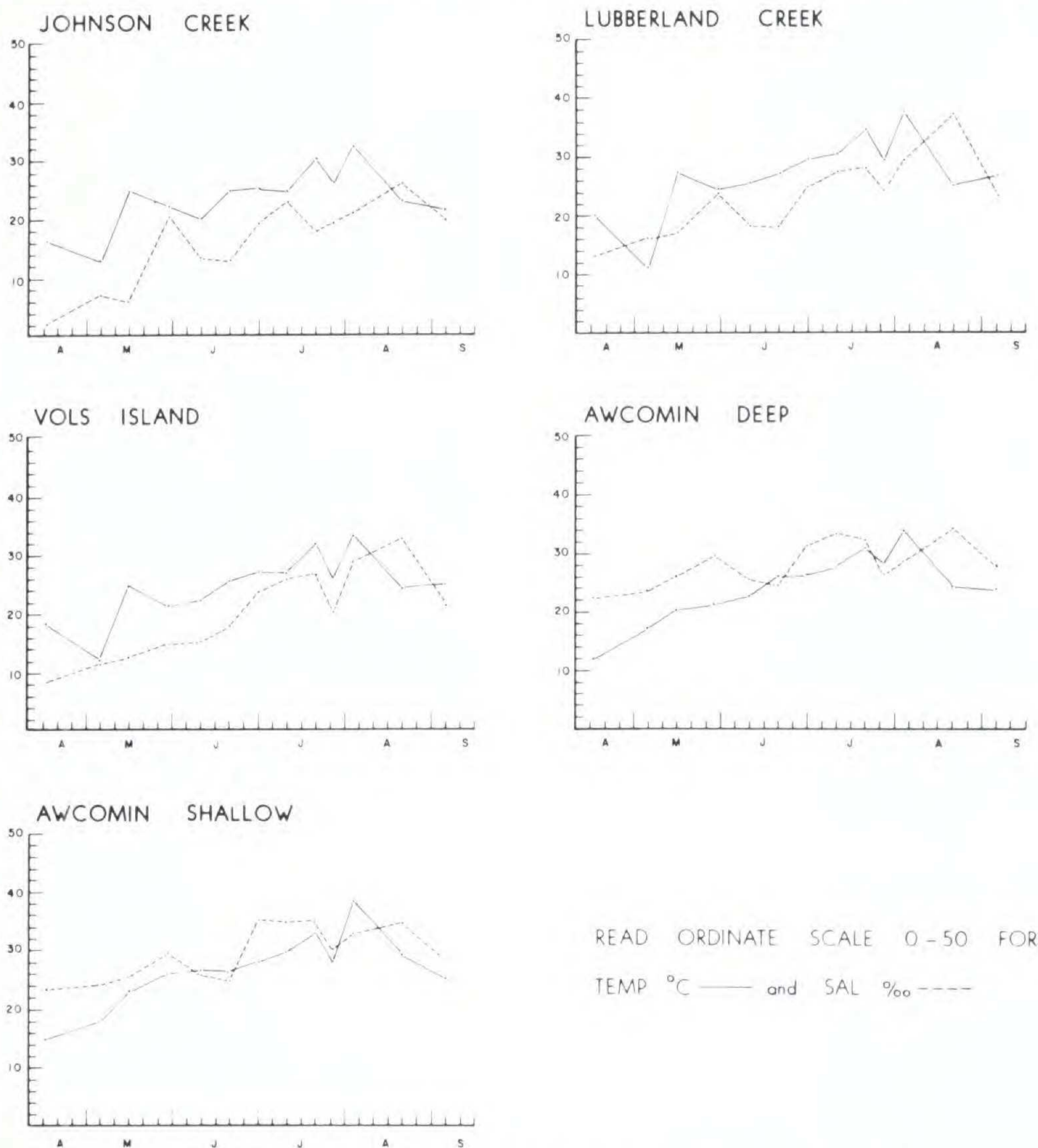


Figure 3. Seasonal water temperature and salinity patterns at five sites April–September 1975.

Table 2. Dissolved oxygen values ($\text{mg}\cdot\text{L}^{-1}$) and percent oxygen saturation (% Sat.) for five sites May-September 1975

Date	JOHNSON CREEK		LUBBERLAND CREEK		VOLS ISLAND		AWCOMIN (DEEP)		AWCOMIN (SHALLOW)	
	$\text{mg}\cdot\text{L}^{-1}$	%Sat	$\text{mg}\cdot\text{L}^{-1}$	%Sat	$\text{mg}\cdot\text{L}^{-1}$	%Sat	$\text{mg}\cdot\text{L}^{-1}$	%Sat	$\text{mg}\cdot\text{L}^{-1}$	%Sat
5- 5	4.2	40.4	11.2	112.1	7.8	75.8	-	-	-	-
5-15	7.9	97.4	20.1	271.9	12.4	157.5	8.6	104.4	8.2	106.9
5-28	7.9	102.1	19.4	272.7	17.8	236.8	9.4	127.9	9.4	152.9
6-10	11.5	142.4	15.8	223.8	15.9	217.1	9.4	130.9	10.5	152.9
6-20	10.5	138.9	14.4	199.9	14.2	198.3	7.5	106.5	9.4	135.0
6-30	13.8	195.9	17.2	256.8	20.7	307.4	10.7	158.3	9.7	151.0
7- 9	11.8	171.2	15.1	238.6	11.5	182.7	3.2	49.8	6.5	102.3
7-19	16.7	256.8	10.0	166.5	3.6	60.3	8.5	131.8	8.6	144.9
7-26	15.7	222.4	13.3	201.3	6.6	97.2	6.5	93.5	8.9	133.0
8- 2	5.6	88.9	10.1	178.9	0.0	0.0	9.0	148.7	10.3	188.2
8-20	5.4	76.8	10.0	149.8	11.0	162.3	9.1	132.9	9.9	156.2
9- 4	9.0	118.9	6.9	97.4	8.4	119.0	7.1	100.5	7.7	109.0

anthesis and fruiting. Setchell recorded optimal ranges of 15–20° C for germination and seedling development and 20–25° C for vegetative growth and reproductive activity; anthesis was slow and eventually ceased after prolonged periods above 25° C. He concluded that temperature was the environmental parameter which most affected growth and development of *Ruppia*.

In a study of the benthic plant composition of a salt pond in Rhode Island, Conover (1966) reported a thermal range of 12–18° C to be optimal for rapid vegetative growth, while 18–22° C was conducive to reproduction. Conover also states that senescence of the *Ruppia* populations is coincident with the seasonal thermal maximum and suggests that since growth of the older tissues and organs begins to diminish in vigor during this time period, temperature had a kinetic effect upon growth.

Anderson (1969) examined the effects of heated water effluent from an electrical generating station of the Patuxent River, Maryland, as a factor related to the disappearance of a large population of *Ruppia maritima*. He found that *R. maritima* and *Potamogeton pectinatus* L. were capable of physiological adjustment to higher temperatures as the leaves matured, and that *Potamogeton* replaced *Ruppia* at 30–35° C.

Conover (1958) found the maximum growth rate of benthic marine plants (including *Ruppia*) in Cape Cod estuaries to occur during the thermal maximum in July and August rather than during the solar maximum. Such is not the case with the *Ruppia* populations in New Hampshire. The growth rate is at a maximum in mid-to late June during the solar maximum, gradually decreasing in July with the plants becoming senescent in late August. Increasing temperature, salinity, growth and attrition of epiphytes, and algal mats all have a limiting effect on growth of the *Ruppia* populations following the late June to mid-July flowering and fruiting maxima. High water temperatures may increase respiration rates, thereby reducing net growth (Conover, 1964).

Temperature stratification in the water column was observed to be more a result of the shading effects of surface algal mats and vegetation density than of depth alone. In the deepest pool at the Awcomin Marsh, with sparse surface cover and submersed vegetation, the water column remained nearly isothermal and isohaline throughout the season. The algal mats probably interfere with convection currents that would otherwise equalize the temperature

(Young & Zimmerman, 1956). Inverse temperature stratification was noted in early spring before algal mats and seedlings developed. This was apparently due to heating of the dark colored bottom sediments by direct insolation.

Boyd (1975) noted that in unshaded pools 51 cm deep the change in temperature from top to bottom seldom exceeded 2.8° C, while in shaded pools (covered with duckweeds) the temperature differential ranged from 5–10° C during the day. Butler (1963) noted that temperature stratification was more pronounced in turbid than in clear ponds of similar size and morphology.

Dale and Gillespie (1977, 1978) found temperature gradients in shallow water bodies to be influenced by submersed aquatic plants as a function of leaf area index and arrangement of leaves, and by the ratio of solar radiation to wind speed. Steep temperature gradients indicate interception of light energy near the surface of the water column by the plants. Sparse vegetation allows a more even distribution of the energy, with the system tending toward isothermy.

My observations suggest that temperature stratification may influence significantly the seed production and germination capacity of *Ruppia* populations. Flowering, fruiting, and seed production in *Ruppia* take place over a longer period in pools where surface algal mats and dense vegetation cause stratification and microthermoclines, than in those pools with isothermal conditions. There is evidence that seeds produced early in the season develop thicker seed coats than those produced later in the season (Mayer, 1969). A seed crop with a range of seed coat thicknesses would surely germinate over a longer period and under a wider range of conditions than would a crop with seed coats of uniform thickness. This may be an adaptation through which populations of an annual reproductive strategy are perpetuated successfully.

Salinity: The salinity characteristics of the *Ruppia* habitats are a function of : (1) tidal flooding; (2) precipitation; (3) evaporation; (4) interchange of water between the substrate and the overlying water; (5) upland runoff.

Many factors interact to determine the frequency of tidal flooding at various sites. Among these are: (1) proximity to drainage ditches or creeks; (2) isolation by levees along water courses; (3) the elevation and micro-relief of the marsh; (4) surface vegetation.

Fluctuations of salinity and temperature in the water column were larger at the estuarine sites than at the coastal sites. Tidal waters entering a panne or pool after a period of wet weather will increase the salinity. Tidal waters entering a panne or pool after a period of drying may appreciably decrease the salinity (Fig. 4). During periods of drying in 1974 the water in many shallow pannes completely evaporated (e.g., Lubberland Creek). Residual water trapped in depressions under algal mats had extremely high salinity (50–70 ‰). Twenty-four hours after tidal flooding the bottom salinity in a panne at Lubberland Creek dropped to 36 ‰ and the surface water was 28 ‰ in 15 cm of water. When heavy rainfall and flooding occur simultaneously after prolonged drying the layering may be even more pronounced provided winds have not accelerated the mixing.

At Johnson Creek and Vols Island, where salinity fluctuations in the water column were substantial, the proximity of the pools to an upland slope suggests that drainage or runoff may be influential in the salinity regime. Nicol (1935) reported that upland drainage of rainfall has an indirect effect on the salinity of salt marsh pools. Many of my observations concur with hers. Fresh water runoff and transference through the peat may be affected by silt-clay or sandy lenses in much the same way that subterranean drainage through upland soils is affected by hard-pans. These lenses are deposits of material from the embayment or creek bottom which were washed up over the marsh surface during violent storms coincident with flooding tides. As subsequent vertical accretion of the peat takes place these lenses become buried in the marsh strata (see Breeding, et al., 1974). Upland runoff may follow the course of these lenses and when they are continuous across the marsh, they may feed directly into the pools.

Ruppia will tolerate a wide range of salinities. Hypertonic death experiments with benthic plants conducted by Conover (1964) indicate that, in general, plant populations found in environments subject to salinity extremes are capable of adapting by some physiological mechanism. He reported *Ruppia* growing in a salinity range of 0–60 ‰. Graves (1908) classified *Ruppia* as a brackish water plant liable to plasmolysis in salinities above 30 ‰. Davis and Tomlinson (1974) described a species of *Ruppia* in Western Australia growing in a salinity range of 92–132 ‰. Mayer (1967, 1969)

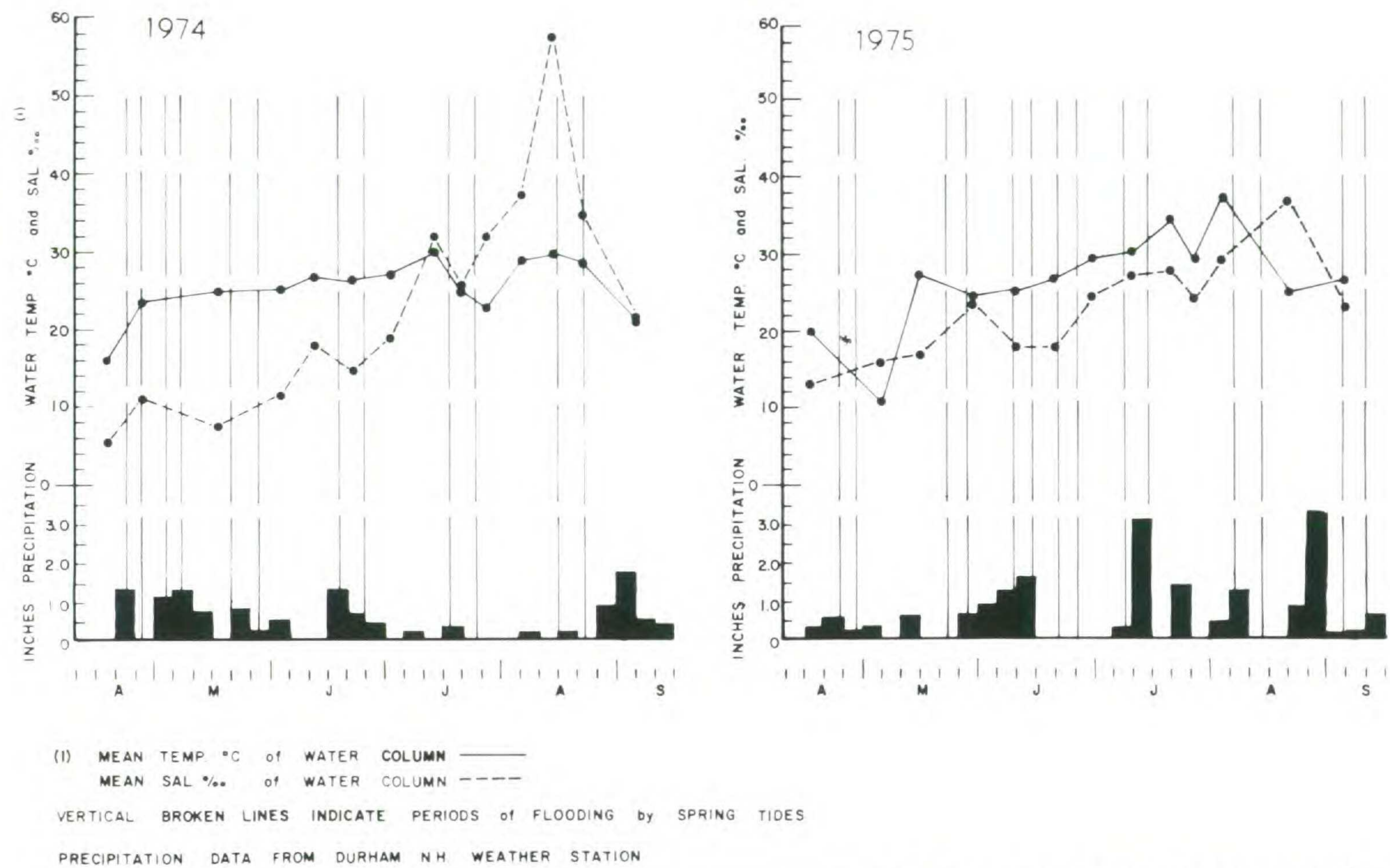


Figure 4. The effect of precipitation and tidal flooding on water temperature and salinity at the Lubberland Creek site 1974 and 1975.

described *Ruppia* as an obligate halophyte, dependent on salinity for growth and development, but requiring low salinity for maximum germination. He found the germination rate to be highest in fresh water with inhibition at 18 ‰ salinity.

Mayer noted that different salinities affected fruit size and shape. In his experiment, seeds produced by plants grown in salinities up to 12 ‰ correspond to var. *obliqua* and have a relatively thick seed coat, while those plants grown at 24–27 ‰ produced seeds corresponding to var. *rostrata* with relatively thin seed coats. I observed a wide range in seed morphology within the same population and often on the same plant throughout the periods of fruit development and seed production. McKay (1935) reported that total salt concentration may influence flowering and fruiting in *Ruppia* more than other parameters.

I found a gradient of salinity regimes in the *Ruppia* habitats. The Johnson Creek site, furthest from direct tidal influence, had a seasonal mean salinity of 15 ‰. The site receives upland runoff from a nearby wooded slope which probably decreases the salinity, especially in early spring when only 2 ‰ salinity was recorded. Lubberland Creek and Vols Island, both of which are in proximity to Great Bay and subject to flooding by more saline waters, had seasonal mean salinities of 22 ‰. At the coastal Awcomin marsh sites salinities averaged 31 ‰ with virtually no influence from fresh water sources.

Ruppia populations distributed along a salinity gradient exhibited clinal variation and adaptation in reproductive strategy. Annual populations are best suited for areas where low salinities in early spring facilitate rapid germination and seedling establishment. Annual populations undergo vigorous vegetative growth, flower, fruit and produce abundant seed before the seasonal salinity maximum occurs. A perennial reproductive strategy has evidently evolved in more saline environments where conditions are not conducive to germination and seedling development. The results of the present study show, however, that for large populations of *Ruppia* in the coastal habitats of New Hampshire, a perennial strategy does not assure continued seasonal growth. The recent disappearance of these populations is more likely the result of a complex of factors of which salinity may be only one. Setchell (1946) observed that the appearance and disappearance of *Ruppia* populations on California

coastal marshes corresponds to variations in conditions of the habitat, and probably are affected most significantly by changes in temperature and salinity.

Oxygen content: During the 1975 season, dissolved oxygen content was recorded at each visit to the five regularly sampled sites. Because each site was sampled at approximately the same time of day throughout the season, the dissolved oxygen patterns indicate the trend in community metabolism at each site (Fig. 5). The values expressed for D.O. and percent oxygen saturation (Table 2) indicate the presence of oxygen including and in excess of that produced by *Ruppia*. Evolution of oxygen by surface mats of filamentous algae, epiphytic, planktonic, and benthic algae are also included in these values.

An oxygen profile is affected by a number of factors including: (1) shading by the algal mats and *Ruppia*; (2) temperature and salinity differences; (3) community respiration and microbial decomposition of senescent vegetation; (4) metabolism at the mud-water interface and in the sediments; (5) gains and losses at the air-water interface (see Sculthorpe, 1967). At sites with limited light penetration due to a dense algal mat or a canopy of *Ruppia*, maximum rates of photosynthesis will occur at or near the surface, whereas in areas with a more uniform distribution and lower density of vegetation in the water column this effect is diminished. It has been shown that in dense stands of aquatic plants in which little mixing of the water takes place, D.O. concentrations may fall sharply with depth and become stratified (Boyd, 1975; Buscemi, 1958).

In the ecocline of *Ruppia* populations on New Hampshire tidal marshes, sites having comparable salinity regimes exhibit similar seasonal oxygen patterns (Fig. 5). The pattern for Johnson Creek is unique in that a series of increases and decreases took place until maximum oxygen concentrations were reached in mid-July (16.7 mg.L⁻¹ O₂; 256.8% O₂ saturation). At this time the pool had maximum algal mat cover and the *Ruppia* population was flowering and fruiting. Senescence of *Ruppia* and the algal mats followed shortly and with subsequent drying conditions the oxygen values dropped sharply. The Lubberland Creek and Vols Island sites, both in proximity to Great Bay, had very similar oxygen patterns. At both sites oxygen concentration initially increased and then decreased in mid-June. This mid-June minimum occurred at all sites and is related to a period of cloudiness and intermittent sun. Oxygen content at Vols

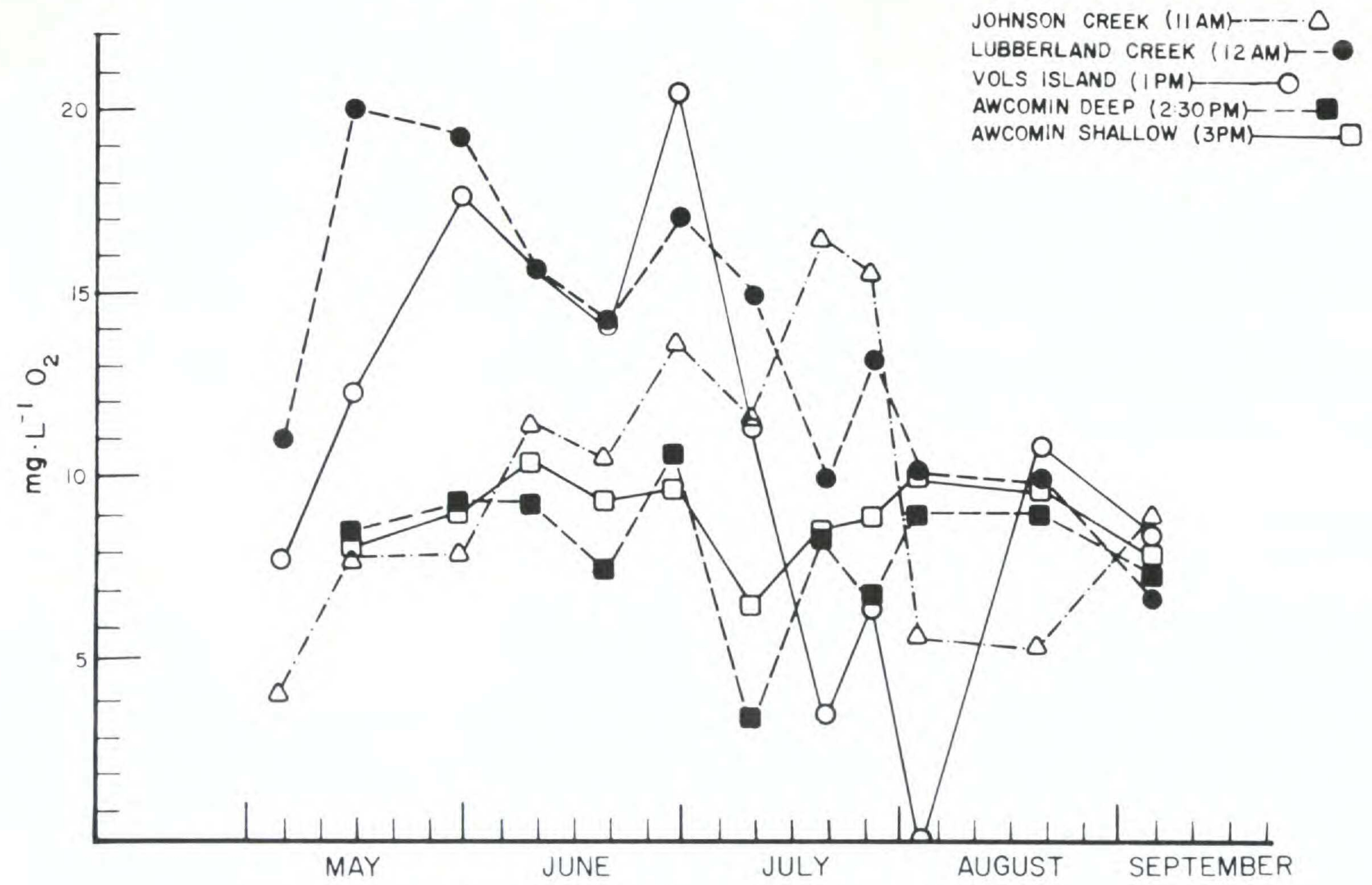


Figure 5. Seasonal dissolved oxygen patterns at five sites May-September 1975.

Table 3. Phenological data for *Ruppia* at five sites April–September 1974

DATE	PHOTO PERIOD	JOHNSON CREEK	LUBBERLAND CREEK	VOLS ISLAND	AWCOMIN (DEEP)	AWCOMIN (SHALLOW)
4-18	13hr 37min	Perennating rhizomes Germination begins	Germination begins		Perennating rhizomes	Perennating rhizomes
4-27			All growth from seed	Germination begins		Scattered seedlings
5-18	14hr 52min	10% algal mat cover Seedlings developing inflorescences	40% algal mat cover	All growth from seed	Scattered seedlings	
6-3		Perennating plants in flower Underwater pollination	Seedlings developing inflorescences	Seedlings developing inflorescences		Perennating plants developing inflorescences Flowering
6-12	15hr 27min	Perennating plants in fruit Seedlings in flower	Flowering Underwater pollination	40% algal mat cover Flowering, underwater pollination	Perennating plants developing inflorescences Flowering	Surface pollination
6-22		50% algal mat cover	80% algal mat cover		30% algal mat cover	Fruit development Dense growth of epiphytes
7-2	15hr 25min	Seedlings underwater pollination and fruit development	Abundant fruit development	Abundant fruit development	Perennating plants Surface pollination	

Table 3 (continued)

7-13			Drying conditions in shallow areas	80-90% algal mat cover	Surface pollina- tion Very little fruit development	Period of drying evaporation of shallow areas
7-20	15hr 02min		Abundant mature fruit			
7-27		Abundant fruit development for entire population	Plants becoming senescent Seed production	Abundant Mature fruit	Plants becoming senescent Dense growth of epiphytes	Plants becoming senescent
8-6	14hr 23min	Abundant mature fruit Algal mats decomposing	Algal mats decomposing Very abundant sulfur bacteria	Pool nearly evaporated	Many inflores- cences No fruit development	Period of drying Very abundant sulfur bacteria
8-14		Plants becoming senescent Very abundant sulfur bacteria	Abundant seed All plants dead Extreme drying	Plants becoming senescent Seed production	No seed production	All plants dead No seed production
8-22	13hr 49min	Seed production		All plants dead	Algal mats decomposing	
9-6		All plants senescent Further increase in sulfur bacteria growth		Very abundant sulfur bacteria and chalky-white precipitate	All plants senescent	

Island reached a maximum in late June when the highest value for any site was recorded ($20.7 \text{ mg.L}^{-1} \text{ O}_2$; 307.4% O_2 saturation), then decreased markedly in July, and the pool became anoxic in early August. The two Awcomin marsh sites had nearly identical oxygen concentration patterns which were the lowest average value of all sites, due, no doubt, to the paucity of submersed and floating vegetation.

Ruppia, like most submersed vascular hydrophytes, retains a percentage of the oxygen produced in photosynthesis within the lacunar system for utilization in respiration (Hartman & Brown, 1967; Sculthorpe, 1967). The gas in the lacunar system of *Ruppia* functions in anther dehiscence and pollination, especially in those plants having underwater pollination (Richardson, 1976b). I have demonstrated, through time-lapse cinemicroscopy and extensive anatomical observations, the nature of an underwater pollination mechanism in *Ruppia*. Anatomical, morphological, and physiological variation in the floral biology of underwater and surface pollinating plants reveal adaptations which are no doubt of evolutionary significance in the genus *Ruppia*. A detailed report of these phenomena will be the subject of another publication.

Turbidity, epiphytes, and algal mats: These three components of the *Ruppia* habitat were found to influence significantly growth, development, and seasonal periodicity of the *Ruppia* populations. Turbidity, which often appeared as a yellow to brownish coloration of the water, was attributed to: (1) dissolved organic matter derived from the substrate; (2) the concentration of organic and inorganic particulate matter in suspension due to roiling of the sediments by wind, tidal action, and fauna (e.g., crabs, fish, and worms); (3) the concentration of phyto- and zooplankton (see Sculthorpe, 1967). Sites with dense populations of *Ruppia* were occasionally turbid due largely to climatic effects and tidal flooding. Sites with sparse vegetation were frequently to consistently turbid due to a combination of the factors enumerated above and the lack of a substrate (submersed vegetation) for epiphytic attachment and settling of particulate matter.

At some sites (e.g., the Awcomin Marsh in 1975) masses of detrital material were observed to float up from the bottom and disperse over the surface of the pool. This may be attributed to the release of gases produced in the sediments and subsequent buoyancy of superficial sediments (Edwards, 1957). Anderson (1970) found *Ruppia* to be sensitive to turbidity and reported that large populations disap-

peared as a result of a rapid increase in turbidity. Boyd (1975) noted that turbidity attributed to plankton and suspended particulate matter can significantly lower the light available for photosynthesis and inhibit the daytime production of photosynthate. Joanen (1964) reported that turbidity caused by wave action, fish, and crabs could inhibit or prevent the growth of *Ruppia*. Phillips (1960) also reported that the disappearance of large populations of *Ruppia* was due to an increase in turbidity. Conover (1966) found that seasonal winds roiling the bottom sediments, which were thereby put into suspension, was more influential than living planktonic bodies in causing turbidity in shallow lagoons. Gutierrez (1977) found that turbidity influenced the competitive capacity of *Ruppia* in a given area, with high turbidity causing mortality or limiting growth to rhizomes, while clearer water was conducive to vigorous growth and flowering.

At sites where dense mats of filamentous algae developed during the growing season the water underlying the algal mats and canopy of *Ruppia* was usually clear. The surface vegetation no doubt diminished the effect of the wind in roiling the sediments, while shading limited the growth of plankton (see Boyd, 1975). Growth of epiphytes and the total accumulation of epibiota were reduced significantly in areas with surface algal mats and *Ruppia* canopies. At Lubberland Creek and similar habitats numerous small snails of the genus *Hydrobia* were seen grazing the epibiota present on *Ruppia* plants under the algal mats to the extent that the plants were nearly free of epibiota throughout most of the season.

Graves (1908), Johnson and York (1915), and Sculthorpe (1967) have shown that the anatomical leaf structure of *Ruppia* is similar to that of shade tolerant plants (e.g., absence of a cuticle; concentration of chloroplasts in epidermal layers). My observations show that the growth of *Ruppia* is more vigorous, and that fruit production is greatly increased, in areas where the plants are partially shaded by surface mats of algae and free of epibiota. At sites where algal mats were scant, epibiota accumulated on the stems and leaves. I found that if the epibiotic layer was stripped off early in the growing season the plants were green, but later in the season they became chlorotic, eventually taking on a pallid, yellow appearance. Sullivan (1976) has examined an epiphytic diatom community on *Ruppia* and found that the marsh sediments were the major source of colonizing cells.

Table 4. Phenological data for *Ruppia* at five sites April–September 1975

DATE	PHOTO PERIOD	JOHNSON CREEK	LUBBERLAND CREEK	VOLS ISLAND	AWCOMIN (DEEP)	AWCOMIN (SHALLOW)
4-16	13hr 28min	Germination begins No rhizomatous growth	Germination began 3-28 Perennating rhizomes along ditches	Germination begins	Fragments of rhizomatous growth	No sign of reestablishment
5-5		All growth from seed	Very abundant seedlings	All growth from seed		
5-15	14hr 46min	Seedlings developing inflorescences	Perennating plants developing inflorescences	50% algal mat cover		
5-28		30% algal mat cover	50% algal mat cover Seedlings developing inflorescences	Scattered seedlings developing inflorescences	No seedlings Very scant vegetative growth	No seedlings
6-10	15hr 25min	Flowering Underwater pollination/fruit development	All plants in flower Underwater pollination/fruit development	Flowering Underwater pollination/fruit development		
6-20			70% dense algal mat cover Sulfur bacteria	95% algal mat cover	10% algal mat cover along edges High turbidity	No sign of vegetative growth Very high turbidity

Table 4 (continued)

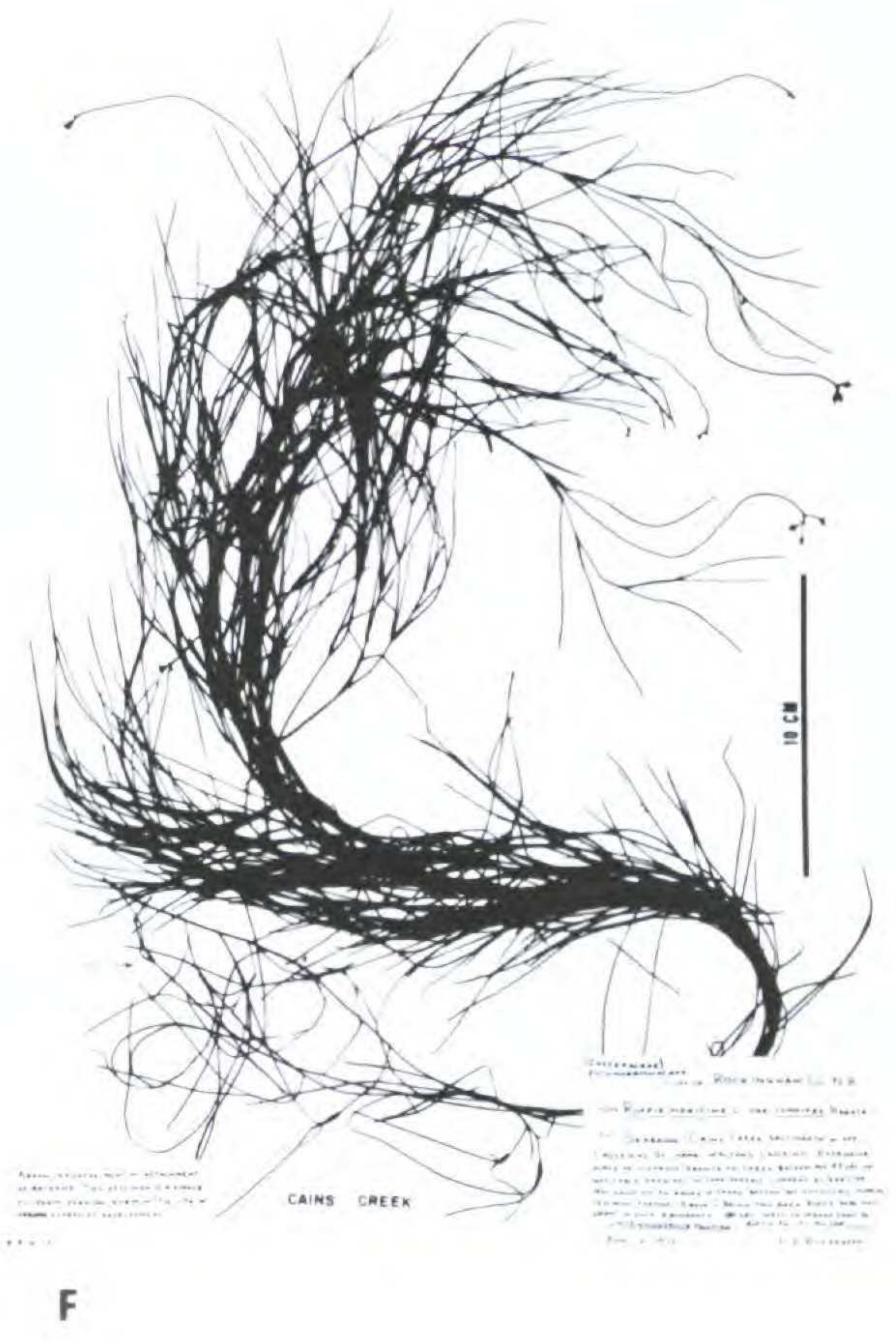
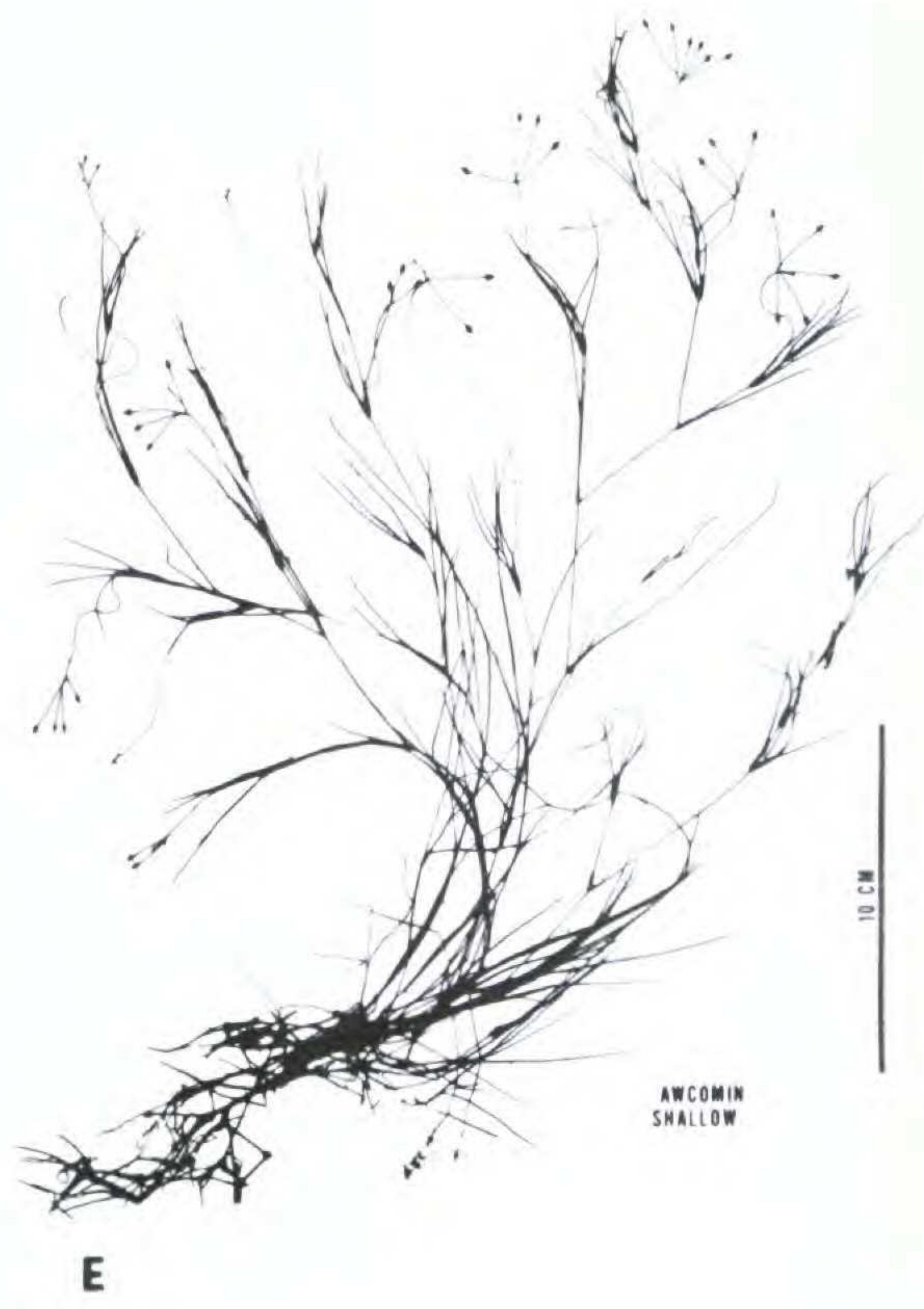
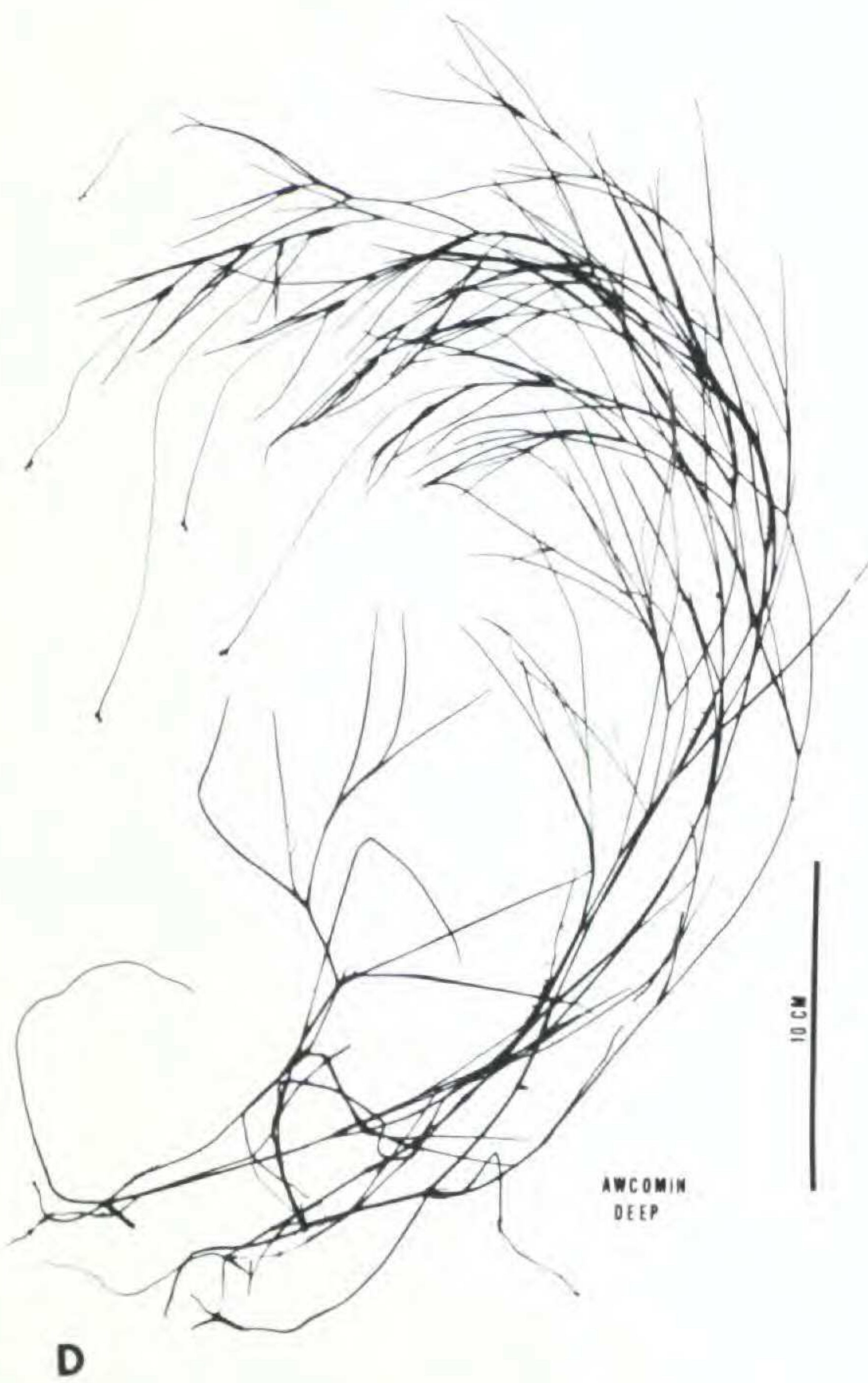
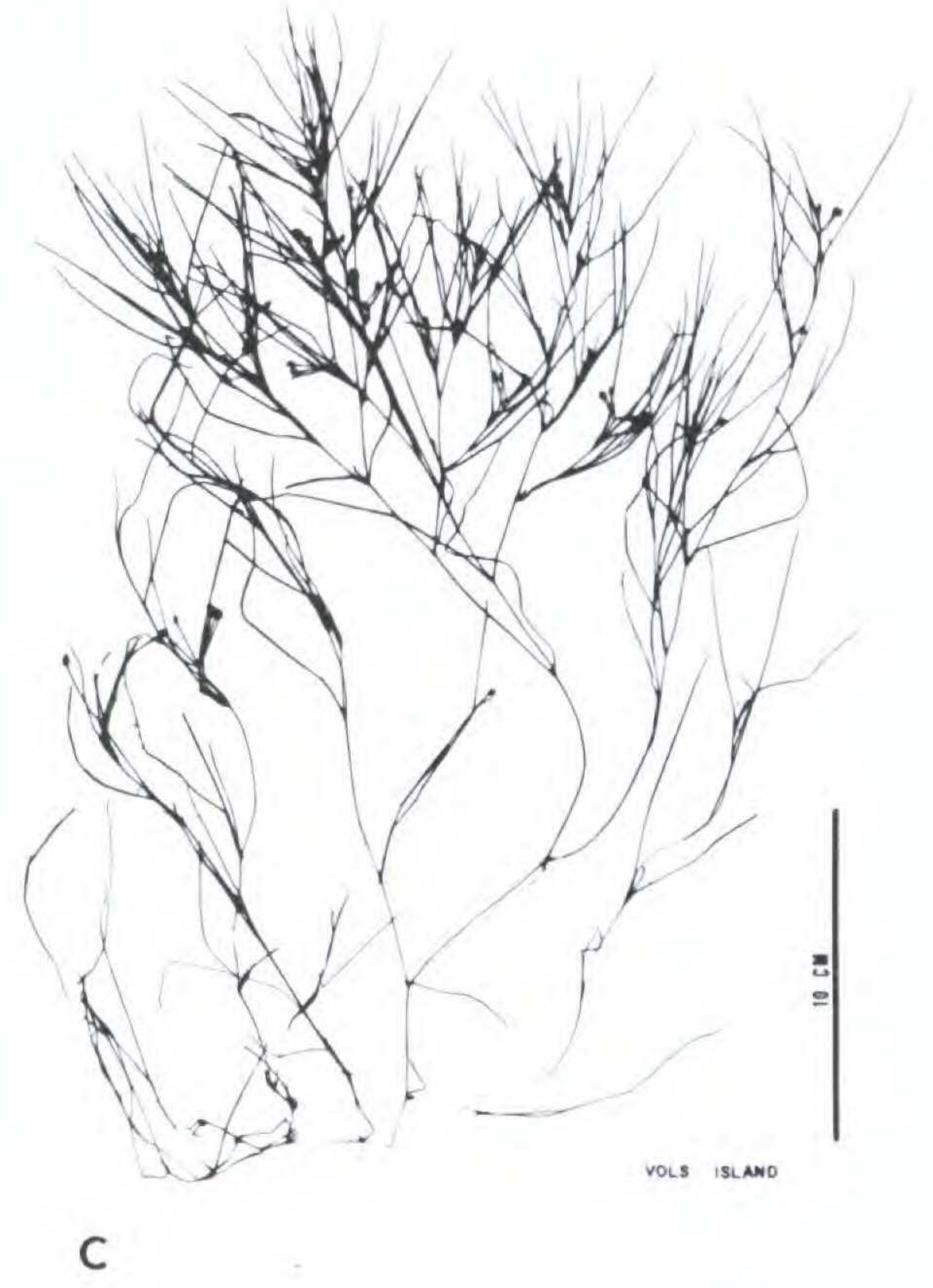
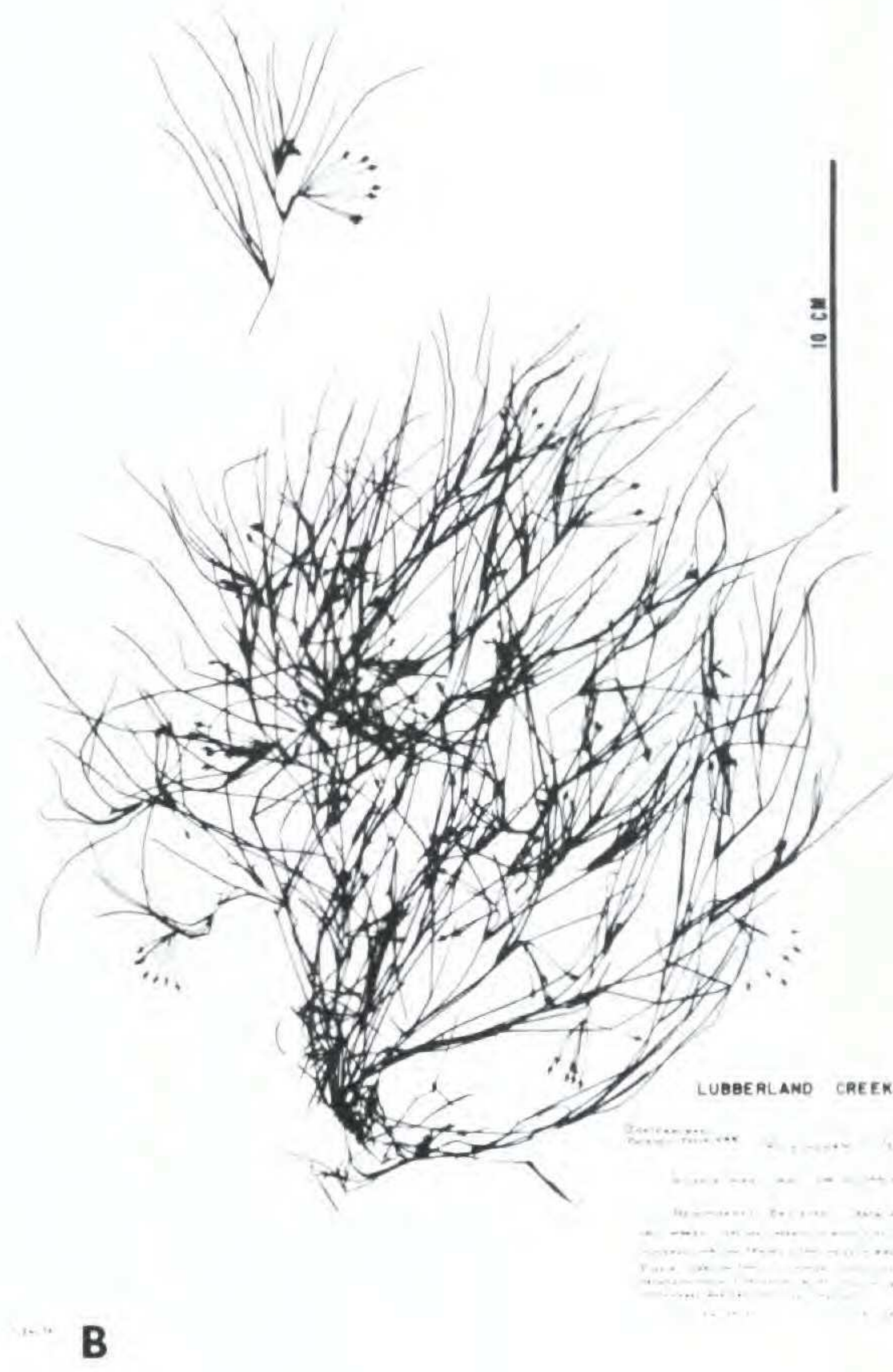
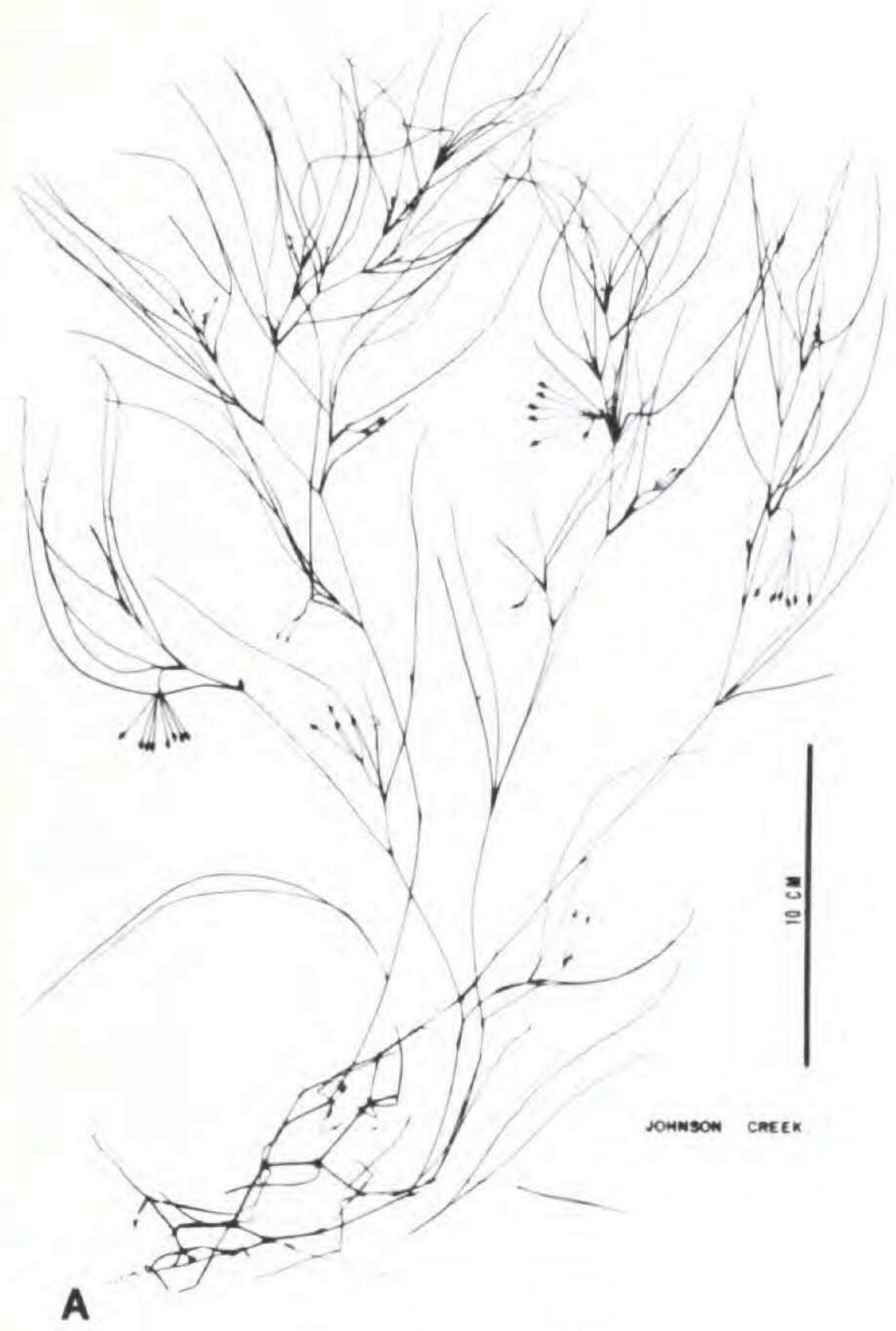
6-30	15hr 27min	90% algal mat cover	Very dense growth abundantly fruiting plants	Drying conditions Maturing fruit Abundant sulfur bacteria		
7-9			Drying conditions Reduction of algal mat cover		No growth High turbidity Abundant sulfur bacteria	No growth High turbidity Abundant sulfur bacteria
7-19	15hr 03min	Abundant mature fruit	Abundant mature fruit Abundant sulfur bacteria	Sparse mature fruit		
7-26		Initial signs of senescence		Drying conditions Plants becoming senescent		Extremely abundant sulfur bacteria
8-2	14hr 36min	Drying conditions	Seed production Algal mats decomposing	Limited seed production		
8-20		Seed production Abundant sulfur bacteria	Plants senescent Very abundant sulfur bacteria	Plants senescent		
9-4	13hr 09min	Very thick algal mat decomposing Very abundant sulfur bacteria Plants senescent		100% cover algal mat decomposing Very abundant sulfur bacteria		

The effects of epibiota on the growth, development, and reproductive capacity of *Ruppia* may be quite significant. Sand-Jensen (1977) reported that epiphytes reduce the photosynthetic rate of *Zostera marina* L. leaves by acting as a barrier to carbon uptake and by reducing light intensity. The dense growth and accumulation of epiphytic material on *Ruppia* plants may inhibit photosynthesis to the extent that (1) not enough oxygen would be produced and stored in the lacunar system to allow for night-time respiration in an environment where the oxygen demand is very high, and (2) production of photosynthate might be limited to the extent that sufficient storage products would not be available to maintain perennating rhizomes or that seed produced might be non-viable. *Ruppia* plants of either annual or perennial reproductive strategy are susceptible to the adverse effects of epibiota.

Epibiota may also limit nutrient availability to the vascular hydrophyte. *Ruppia* is more dependent upon hydrological than edaphic properties of the environment for nutrient assimilation (Conover, 1958, 1964, 1966; Conover & Gough, 1966; Graves, 1908; Sculthorpe, 1967). The rate of transfer of required gases and dissolved nutrients from the water into the plant is a function of the rate of movement of water over the leaf and stem surfaces (Conover, 1966). My observations support these findings. The most vigorous growth of *Ruppia* found during this study was that at Cains Creek (a coastal site, see Fig. 1) where the velocity of the water current is considerable as the tide rises and falls daily. These plants were almost free of epibiota and had a very dark-green robust appearance (Fig. 9,F). Conover and Gough reported that nutrient uptake by the leaves of *Ruppia* and *Zostera marina* L. will vary with the season because epiphyte growth apparently reduces the assimilation efficiency of the epidermis.

Conover and Gough found root growth and development in *Ruppia* and *Zostera* to be directly related to the type of sedimentary environment. In the highly reducing sedimentary environments characteristic of most *Ruppia* habitats, oxygen supply to the roots is essential. Dense epibiota, in limiting photosynthesis, would limit the amount of oxygen available for diffusion through the lacunar system to the roots. The effect was apparent at a number of sites where

Figure 9. Growth habit of mature *Ruppia maritima* L. plants from six sites: A, Johnson Creek; B, Lubberland Creek; C, Vols Island; D, Awcomin Marsh (deep pool); E, Awcomin Marsh (shallow pool); F, Cains Creek



roots became flaccid, chalky white and rotted in appearance. Verhoeven (1978) reports that after four months of growth, the basal parts of *Ruppia cirrhosa* stems start to decay, the dense vegetation above the substrate gradually loses contact with the rooting parts, with senescence and complete detachment rapidly following. This process occurred at most sites in the New Hampshire marshes and was coincident with a marked increase on the plants and substrate of bacteria which produce or utilize hydrogen sulfide.

During the summers of 1977 and 1978 while collecting information on adaptation and variation in *Ruppia* populations, I noted that plants were again well established at sites where they had been absent for from one to three years (i.e., Awcomin Marsh). The reestablishment of these populations was from seed, indicating the presence of a seed bank in which dormancy has persisted for up to three years. Presently, core samples are being taken in an effort to determine the structure of the seed bank, while further research is necessary to understand the factors controlling seed dormancy and germination in these environments.

Ruppia habitats act as catchment basins for autochthonous and allochthonous organic matter. Pannes and pools are especially well suited for this. Fragments of vegetation from the adjacent marsh are carried into these areas by flood tides, and eventually settle out. This material provides additional substrate for microbial decomposition and the attachment of epibiota. Senescent *Ruppia* plants, epibiota, and the algal mats which decompose in later summer contribute to a detrital reservoir. The material entrained in these areas provides an important source of nutrients (see Nixon & Oviatt, 1973).

Ten Day Study

The Vols Island site was visited for ten consecutive days to record diel and diurnal fluctuations of various parameters (Figs. 6, 7 & 8). The effect of the daily solar radiation load on photosynthesis is directly reflected in fluctuations of dissolved oxygen and percent oxygen saturation (Fig. 6). The degree of eccentricity in the pH envelope, as described by the upper and lower range of the daily measurements, illustrates an effect of photosynthetic depletion of carbon dioxide. Air and water temperatures are directly affected by insolation. The mean water temperature increased daily as evaporation and transference of water into the surrounding peat decreased

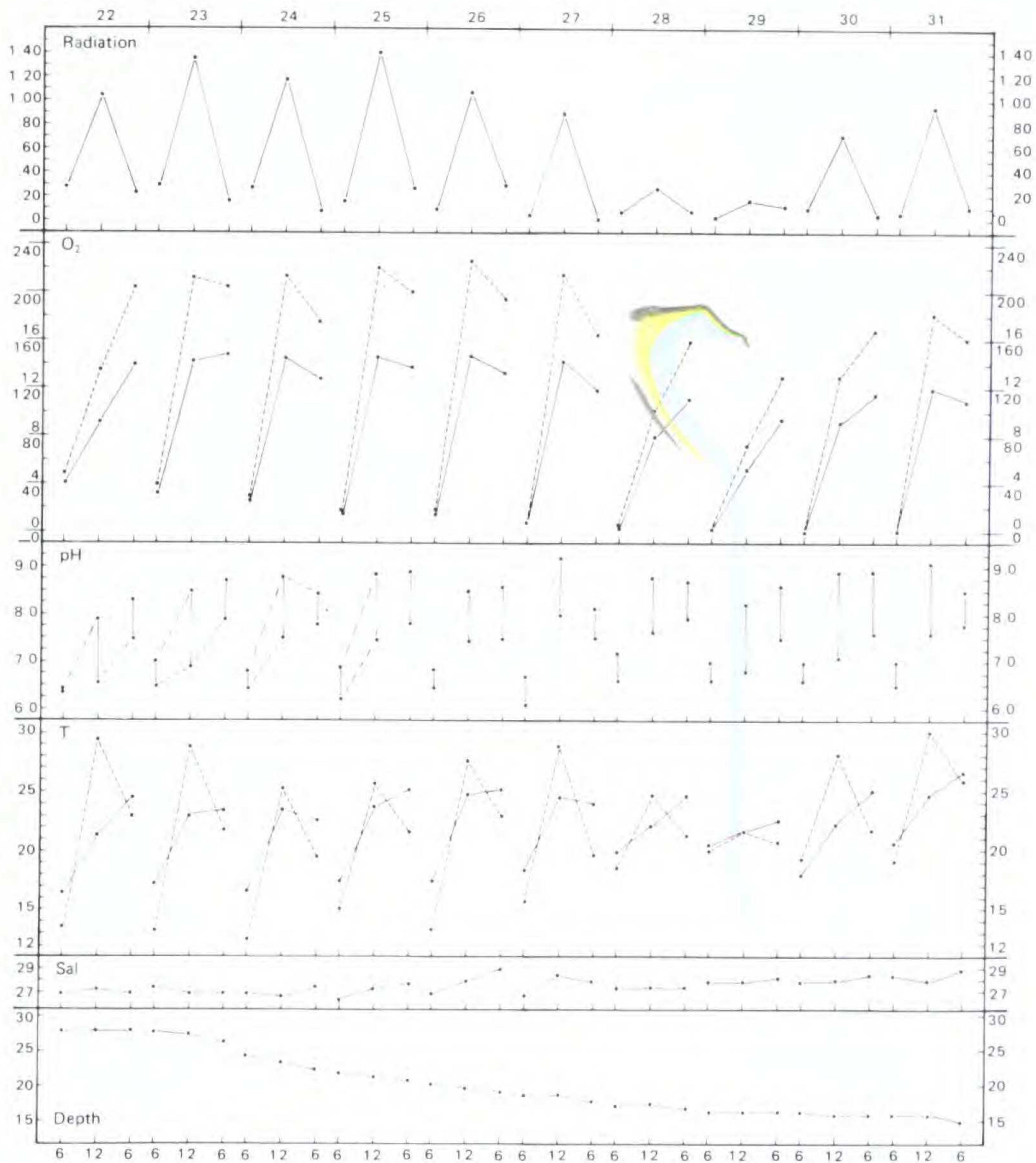


Figure 6. Diurnal fluctuations (6:00 am, noon, and 6 pm) in incident radiation, (readings averaged over 10 minutes), oxygen content ($\text{mg}\cdot\text{L}^{-1}$) O_2 , (solid line, 0–16; % O_2 saturation, broken line, 0–240), hydrogen ion concentration, temperature (air, broken line; mean of water column, solid line), salinity, and depth over ten days (July 22–31, 1974) at the Vols Island site.

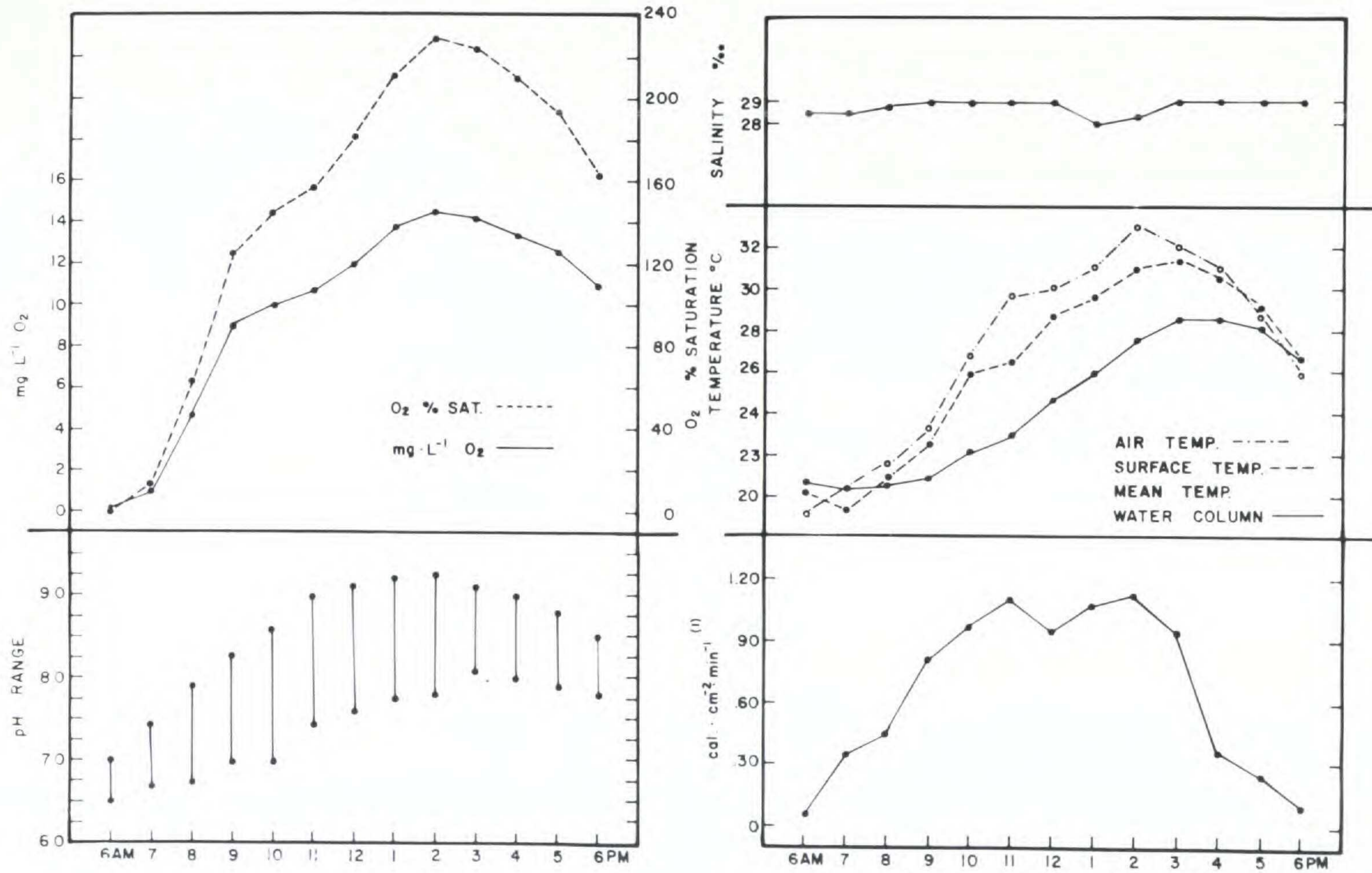
the depth. Only trace amounts of precipitation occurred throughout the study period so that the full effect of drying conditions during a neap tide period was apparent. A marked drop in the water level was noted with only about one-half the initial volume present after ten days. Salinity rose from 27 0/00 to 29 0/00 in a slightly erratic fashion. The most significant feature of the diel changes in the parameters was oxygen depletion, which occurred as the water level dropped and mean water temperature rose. Morning D.O. gradually dropped until the system became anoxic on the ninth and tenth days. Nighttime community respiration and chemical redox reactions apparently depleted the oxygen produced during the day. Because the sky was overcast on the seventh and eighth days, oxygen production was limited.

The curves for both pH and oxygen content coincide with the rise and fall of incident radiation (Fig. 7). There is an apparent time lag between oxygen values and solar radiation. Nixon and Oviatt (1973) reported that throughout the year oxygen curves tended to lag behind solar radiation by about one hour. Nicol (1935) described similar diurnal oxygen curves.

A temperature inversion occurred diurnally in the water column (Fig. 8). In early morning, inverse stratification was noted due to a time lag in heat dissipation within the water column so that the bottom temperature was warmer than the surface. The temperature profile changed as insolation increased, with the greatest fluctuation occurring at the surface and the least at the bottom. The temperature differential from surface to bottom in 15 cm of water was 1.5° C in early morning and 7.5° C by mid-day as the system became highly stratified. As insolation decreased in late afternoon the system tended toward isothermy as the pattern again began to reverse.

CONCLUSIONS

Ruppia maritima L. is a plant of broad ecological amplitude. Persistence of a population in a particular habitat is due to a continuation of conditions favorable to growth and development. Seasonal periodicity and reestablishment of annual or perennial populations are related to ecological succession of the habitats as well as specific environmental parameters. Clinal variation in vegetative morphology and reproductive behavior are apparently expressions of adaptation by *Ruppia* to a diversity of habitats.



(1) INCIDENT RADIATION REPRESENTS AVERAGE OF READINGS OVER TEN MINUTE PERIOD

Figure 7. Diurnal fluctuations (hourly) in incident radiation, oxygen content, hydrogen ion concentration, temperature, salinity and depth over twelve hours (July 31, 1974) at the Vols Island site.

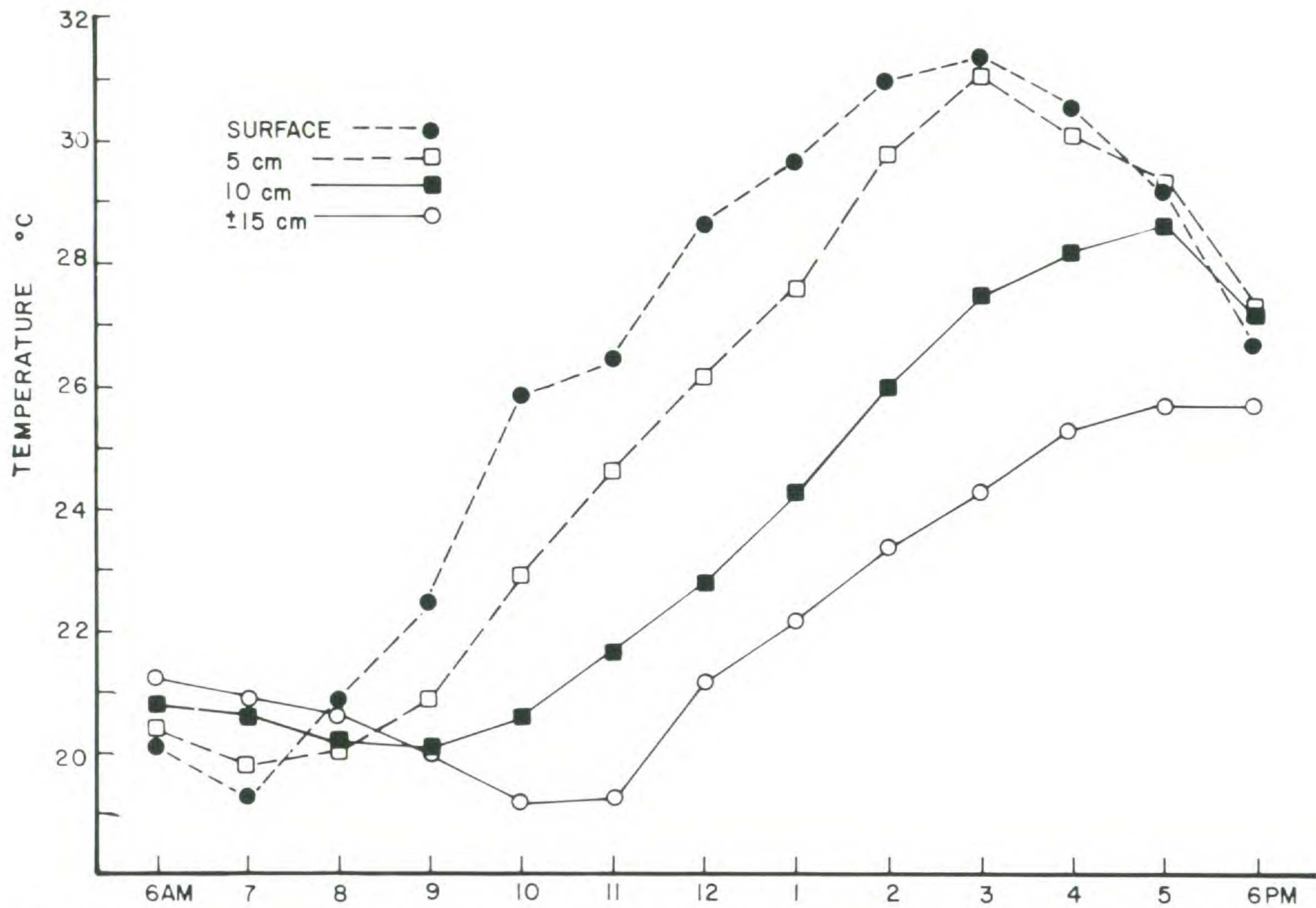


Figure 8. Diurnal fluctuations (hourly) in temperature of the water column (surface, 5 cm, 10 cm, bottom) over twelve hours (July 31, 1974) at the Vols Island site.

ACKNOWLEDGMENTS

Field research for this study was supported in part by U.N.H. Graduate Teaching Assistant Summer Fellowships for July and August of 1974 and 1975. I would like to acknowledge the assistance of Dr. A. Linn Bogle, Dr. Russell S. Kinerson, and Dr. Arthur C. Mathieson, all of the University of New Hampshire, in reviewing the manuscript.

LITERATURE CITED

- ANDERSON, R. R. 1969. Temperature and rooted aquatic plants. *Ches. Sci.* **10**: 157-164.
- . 1970. The submerged vegetation of Chincoteague Bay. p. 136-155 *In*: Assateague Ecological Studies, part I. Environmental Information. Nat. Res. Inst. U. Maryland, Contrib. No. 446.
- ANON. 1974 & 1975. Tide tables high and low water predictions 1974 & 1975 East coast of North America including Greenland. U.S.D.C., N.O.A.A., Nat. Ocean Surv. Washington D.C. 288p.
- A. P. H. A. 1971. Standard methods for the examination of water and wastewater. 13th ed., Amer. Publ. Health Assoc., New York. 874 p.
- BREEDING, C. H. J., F. D. RICHARDSON, & S. A. L. PILGRIM. 1974. Soil survey of New Hampshire tidal marshes. N.H. Agr. Exp. Sta. Res. Rept. No. 40. 94 p. and maps.
- BOURN, W. S. 1935. Sea-water tolerance of *Ruppia maritima* L. Boyce Thompson Inst. Contrib. 7: 249-255.
- BOYD, C. E. 1975. Competition for light by aquatic plants in fish ponds. Auburn Univ. Agr. Exp. Sta. Circ. 215. 19 p.
- BUSCEMI, R. W. 1958. Littoral oxygen depletion produced by a cover of *Elodea canadensis* *Oikos* **9**: 239-245.
- BUTLER, J. L. 1963. Temperature relations in shallow turbid ponds. *Proc. Okla. Acad. Sci.* **43**: 90-95.
- CHAPMAN, V. J. 1938. Coastal movement and development of some New England marshes. *Proc. Geologists' Assoc.* **49**: 373-384.
- . 1940. Succession on the New England salt marshes. *Ecology* **21**: 279-282.
- . 1960. Salt marshes and salt deserts of the world. L. Hill, London. 392 p.
- CONOVER, J. T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. *Texas Univ. Inst. Mar. Sci. Pub.* **5**: 97-147.
- . 1964. The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. *Bot. Mar.* **7**: 4-41.
- . 1966. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. p. 5: 1-5:13. *In*: Tech. Rept. No. 3 Environmental relationships of benthos in salt ponds. Grad. Sch. Oceanography. Univ. R.I.
- . & E. GOUGH. 1966. The importance of stem and leaf vs. root assimilation in *Ruppia maritima* L. and *Zostera marina* L. related to seasonal growth. p. 6:1-6:19. *In*: Tech. Rept. No. 3 Environmental relationships of benthos in salt ponds. Grad. Sch. Oceanography. Univ. R. I.

- CROCKER, W. 1907. The germination of seeds of water plants. *Bot. Gaz.* **44**: 375–380.
- DALE, H. M. & T. J. GILLESPIE. 1977. The influence of submersed aquatic plants on temperature gradients in shallow water bodies. *Can. J. Bot.* **55**: 2216–2225.
- . 1978. Diurnal temperature gradients in shallow water produced by populations of artificial aquatic macrophytes. *Can. J. Bot.* **56**: 1099–1106.
- DAVIS, J. S., & P. B. TOMLINSON. 1974. A new species of *Ruppia* in high salinity in Western Australia. *J. Arnold Arb.* **55**: 59–65.
- EDWARDS, R. W. 1957. Vernal sloughing of sludge deposits in a sewage effluent channel. *Nature (London)* **180**: 100.
- FERNALD, M. L., & K. M. WIEGAND. 1914. The genus *Ruppia* in Eastern North America. *Rhodora* **16**: 119–127.
- GORE, L. F. 1965. Effects of small salt marsh impoundments upon *Ruppia* and macroinvertebrates. M.S. Thesis. U. of Maine, Orono. 111 p.
- GRAVES, A. H. 1908. The morphology of *Ruppia maritima*. *Trans. Conn. Acad. Arts Sci.* **14**: 150–170.
- GUPPY, H. B. 1897. On the postponement of the germination of the seeds of aquatic plants. *Proc. R. Soc. Edinb.* **13**: 344–359.
- GUTIERREZ, M. G. 1977. Observaciones sobre un comportamiento atípico de *Ruppia maritima* L. en una laguna costera tropical. *Bol. Soc. Bot. Mex.* **37**: 53–68.
- HARTMAN, R. T. & D. L. BROWN. 1967. Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. *Ecol.* **48**: 252–258.
- HUTCHINSON, J. 1934. The families of flowering plants. II. Monocotyledons. Macmillan and Co. Ltd., London. 243 p.
- . 1959. The families of flowering plants. 2nd ed. Clarendon Press, Oxford. 792 p.
- JOANEN, J. T. 1964. A study of factors that influence the establishment of natural and artificial stands of wigeon-grass, *Ruppia maritima* L., on Rockefeller Refuge, Cameron Parish, Louisiana. M.S. Thesis. Louisiana State Univ., Baton Rouge. 63 p.
- JOHNSON, D. S., & H. H. YORK. 1915. The relation of plants to tide levels. *Carnegie Inst. Wash. Publ.* **206**. 162 p.
- MAYER, F. L. JR. 1967. The effect of salinity on growth and reproduction of *Ruppia maritima* L. M.S. Thesis. Utah State Univ. 66 p.
- . 1969. Influence of salinity on fruit size in *Ruppia maritima* L. *Proc. Utah Acad. Sci. Arts and Letters.* **46**: 140–143.
- MCKAY, E. 1935. Salt tolerance of *Ruppia maritima* in lakes of high magnesium sulphate content. *Plant Phys.* **10**: 425–446.
- MCLAUGHLIN, E. G. 1974. Autecological studies of three species of *Calitriche* native in California. *Ecol. Monogr.* **44**: 1–16.
- MUENSCHER, E. C. 1936. The germination of the seeds of *Potamogeton*. *Ann. Bot.* **50**: 805–821.
- NICOL, E. A. T. 1935. The ecology of a salt-marsh. *Mar. Biol. Assoc. U.K.* **20**: 203–261.
- NIXON, S. W., & C. A. OVIATT. 1973. Ecology of a New England salt marsh. *Ecol. Monogr.* **43**: 463–498.

- PHILLIPS, R. C. 1960. The ecology of marine plants of Crystal bay Florida. *Quart. J. Florida Acad. Sci.* **23**: 328-337.
- POSLUSZNY, U., & R. SATTLER. 1974. Floral development of *Ruppia maritima* L. var. *maritima*. *Can. J. Bot.* **52**: 1607-1612.
- REDFIELD, A. C. 1959. The Barnstable marsh. p. 37-39. *In*: Proc. Salt Marsh conference, Marine Institute, Univ. Georgia, Athens.
- . 1965. The thermal regime in salt marsh peat at Barnstable, Massachusetts. *Tellus* **17**: 246-258.
- . 1972. Development of a New England salt marsh. *Ecol. Monogr.* **42**: 201-237.
- RICHARDSON, F. D. 1976a. Environmental parameters of *Ruppia maritima* L. populations on New Hampshire tidal marshes. M.S. Thesis. University of New Hampshire. 98 p.
- . 1976b. Pollination mechanism in *Ruppia*. *Helobiae Newsletter*. Melbourne. **1**: 12-15.
- SAND-JENSEN, K. 1977. Effects of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* **3**: 55-63.
- SCULTHORPE, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd. London. 610 p.
- SETCHELL, W. A. 1924. *Ruppia* and its environmental factors. *Proc. Nat. Acad. Sci.* **10**: 286-288.
- . 1946. The genus *Ruppia*. *Proc. Calif. Acad. Sci.* **25**: 469-478.
- STRICKLAND, J. D. H., & T. R. PARSONS. 1968. A practical handbook of sea water analysis. Fish Res. Bd. of Canada. Ottawa. 311 p.
- SULLIVAN, M. J. 1976. Structural characteristics of a diatom community epiphytic on *Ruppia maritima* L. *Phycol. Soc. Amer. Ann. meeting*. Tulane Univ., New Orleans. (Abstr.)
- UHL, N. W. 1947. Studies in the floral morphology and anatomy of certain members of the Helobiae. Ph.D. Thesis. Cornell University. 107 p. and plates.
- VERHOEVEN, J. T. A. 1975. *Ruppia*—communities in the Camargue, France. Distribution and structure in relation to salinity and salinity fluctuations. *Aquat. Bot.*, **1**: 217-241.
- . 1978. Natural regulation of plant biomass in a *Ruppia*-dominated system. *Proc. EWRS 5th Symp. on Aquatic Weeds*. 53-61.
- . & W. VAN VIERSSEN. 1978. Distribution and structure of communities dominated by *Ruppia*, *Zostera* and *Potamogeton* species in the inland waters of "De Bol", Texel, The Netherlands. *Estuarine and Coastal Marine Science*. **6**: 417-428.
- YOUNG, N. F. & J. R. ZIMMERMAN. 1956. Variation in temperature in small aquatic situations. *Ecol.* **37**: 609-611.

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